

## Lemur Traits and Madagascar Ecology: Coping With an Island Environment

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**ABSTRACT** The last decade's lemur research includes successes in discovering new living and extinct species and learning about the distribution, biogeography, physiology, behavior, and ecology of previously little-studied species. In addition, in both the dry forest and rain forest, long-term studies of lemur demography, life history, and reproduction, have been completed in conjunction with data on tree productivity, phenology, and climate. Lemurs contrast with anthropoids in several behavioral features, including female dominance, targeted female-female aggression, lack of sexual dimorphism regardless of mating system, sperm competition coupled with male-male aggression, high infant mortality, cathemerality, and strict seasonal breeding. Hypotheses to explain these traits include the "energy conservation hypothesis" (ECH) suggesting that harsh and unpredictable climate factors on the island of Madagascar have affected the evolution of female dominance, and the "evolutionary disequilibrium hypotheses" (EVDH) suggesting that the recent megafauna extinctions have influenced lemurs to become diurnal. These hypotheses are compared and contrasted in light of recent empirical data on climate, subfossils, and lemur behavior. New data on life histories of the rain forest lemurs at Ranomafana National Park give further support to the ECH. Birth seasons are synchronized within each species, but there is a 6-month distribution of births among species. Gestation and lactation lengths vary among sympatric lemurs, but all lemur species in the rain forest wean in synchrony at the season most likely to have abundant resources. Across-species weaning synchrony seen in Ranomafana corroborates data from the dry forest that late lactation and weaning is the life history event that is the primary focus of the annual schedule. Lemur adaptations may assure maximum offspring survival in this environment with an unpredictable food supply and heavy predation. In conclusion, a more comprehensive energy frugality hypothesis (EFH) is proposed, which postulates that the majority of lemur traits are either adaptations to conserve energy (e.g., low basal metabolic rate (BMR), torpor, sperm competition, small group size, seasonal breeding) or to maximize use of scarce resources (e.g., cathemerality, territoriality, female dominance, fibrous diet, weaning synchrony). Among primates, the isolated adaptive radiation of lemurs on Madagascar may have been uniquely characterized by selection toward efficiency to cope with the harsh and unpredictable island environment. *Yrbk Phys Anthropol* 42:31-72, 1999. © 1999 Wiley-Liss, Inc.

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Two decades ago, Clutton-Brock and Harvey compared the then-existing data on primates to examine sexual selection theory (Clutton-Brock and Harvey, 1977; Clutton-Brock et al., 1977). Trends seen in ungulates, carnivores, and bats were observed in primates. Few lemurs were considered in these early analyses because of scarce data. This comparative approach offered insights into the evolution of sperm competition, infanticide, parental care, the timing of life history events, and sexual dimorphism (Hrdy, 1979, 1981; Harvey et al., 1978; Harvey and Harcourt, 1984; Wright, 1984; Smuts et al., 1987; Dunbar, 1988).

However, when lemurs were studied, they often did not support the predictions derived from anthropoid data. Research results in the last decade on the demography, ecology, and behavior of wild lemurs suggest that lemurs are different from monkeys in nine traits, which have been targeted as “puzzling” or “idiosyncratic.” These traits are: (1) female dominance over males (Pollock, 1979; Richard, 1987; Kappeler, 1990); (2) targeted

female-female aggression (Vick and Pereira, 1989; Taylor, 1986; Hood and Jolly, 1995; Wright, 1995; Pereira and Kappeler, 1997); (3) lack of sexual dimorphism regardless of social system (Kay et al., 1988; Albrecht et al., 1990; Wright, 1993; Kappeler, 1996b; 1997a); (4) many monogamous species (Wright, 1993; van Schaik and Kappeler, 1996; Jolly, 1998); (5) sperm competition combined with male-male aggression (Pereira and Weiss, 1991; Kappeler 1997b); (6) high infant mortality (Sussman, 1991; Richard et al., 1991; Wright, 1995); (7) cathemerality in some species (Overdorff, 1988; Tattersall, 1988; Rasmussen, 1999); (8) low metabolic rate (Daniels, 1984; Richard and Nicoll, 1987; Schmid and Ganzhorn, 1996; Schmid, 1998; Martin, 1990); and (9) strict breeding season entrained by photoperiods (van Horn and Resko, 1977; Rasmussen, 1985).

Lemur research in Madagascar has blossomed during the last decade and a half. Recent successes include discovering new living and extinct species (Tables 1 and 2)

TABLE 1. Families and genera of lemurs, living and extinct<sup>1,2</sup>

Family	Genera	Species	body mass (kg)	Reference
Cheirogaleidae	<i>Cheirogaleus</i> + *	2	0.14–0.45	Wright and Martin, 1995; Muller, 1999
	<i>Microcebus</i> +	3	0.03–0.06	Atsalis et al., 1996
	<i>Mirza</i> +	1	0.30	Kappeler, 1997a
	<i>Phaner</i> +	1	0.46	Kappeler, 1991
	<i>Allocebus</i> +	1	0.09	Meier and Albignac, 1991
Megaladapidae	<i>Lepilemur</i> + *	7	0.54–0.97	Kappeler, 1991; Porter, 1998
	<i>Megaladapis</i> *	3	35.0–75.0	Godfrey et al., 1997a
Lemuridae	<i>Lemur</i> +	1	2.7	Kappeler, 1991
	<i>Eulemur</i> + *	5	1.6–2.4	Simons and Rumpler, 1988
	<i>Varecia</i> + *	1	3.5	Balko, 1998; Vasey, 1998
	<i>Haplemur</i> + *	3	0.9–2.4	Glander et al., 1992; Tan, 1999
	<i>Pachylemur</i> *	2	10.0	Godfrey et al., 1997
Indriidae	<i>Propithecus</i> + *	3	3.3–7.3	Meyers, 1993; Powzyk, 1997
	<i>Indri</i> + *	1	5.8–7.5	Powzyk, 1997
	<i>Avahi</i> + *	1	1.0	Glander et al., 1992
Daubentonidae	<i>Daubentonia</i> + *	2	2.5–10.0	Sterling, 1994; Simons, 1994
Archaeolemuridae	<i>Archaeolemur</i> *	2	17.0–22.0	Godfrey et al., 1997a
	<i>Hadropithecus</i> *	1	28.0	Godfrey et al., 1997a
Palaeopropithecidae	<i>Mesopropithecus</i> *	3	10.0–12.0	Simons et al., 1995
	<i>Babakotia</i> *	1	15.0	Simons et al., 1992
	<i>Palaeopropithecus</i> *	2	35.0–55.0	Godfrey et al., 1997a
	<i>Archaeoindris</i> *	1	200.0	Godfrey et al., 1997a

<sup>1</sup> Adapted from Rowe, 1996; Godfrey et al., 1997a.

<sup>2</sup> Those genera marked with an asterisk are found in the subfossil record; and + are extant. Body mass are genus ranges, including both males and females of the largest and smallest species. Extinct species weights are estimated from morphology.

TABLE 2. *Madagascar lemur species discovered, rediscovered or redescribed from 1987–1997*<sup>1</sup>

Species	Current status	Weight (kg)	Location	Reference
<i>Babakotia radofilai</i>	Extinct	15.00	Ankarana	Simons et al., 1990
<i>Mesopropithecus dolicho-brachion</i>	Extinct	10.00	Ankarana	Godfrey et al., 1995
<i>Haplemur aureus</i> (golden bamboo lemur)	Critically endangered	1.80	Ranomafana Andringitra	Meier et al., 1987a Sterling & Ramarison, 1996
<i>Microcebus ravelobensis</i> (northwestern golden-brown mouse lemur)	Unknown	0.56	Ampijoroa	Zimmerman et al., 1998
<i>Haplemur simus</i> (greater bamboo lemur)	Endangered	2.80	Ranomafana Kianjavato	Wright et al., 1987 Meier et al., 1987b
<i>Allocebus trichotis</i> (hairyeared dwarf lemur)	Critically endangered	0.89	Mananara Anjaraharibe-Sud Zahamena Perinet	Meier & Albignac, 1991 Schmid and Smolker 1997 Rakotoarison et al., 1998 Rakotoarison et al., 1998
<i>Microcebus cf. myoxinus</i> (pygmy mouse lemur)	Endangered	0.30	Kirindy Baly Bay	Schmid and Kappeler, 1994 Hawkins et al., 1998
<i>Propithecus tattersalli</i> (golden-crowned sifaka)	Critically endangered	3.30	Daraina	Simons, 1988
<i>Eulemur collaris</i> (collared lemur)	Critically endangered	2.1	Midongy	Djletati et al., 1997
<i>Eulemur albocollaris</i> (white collared lemur)	Critically endangered	2.1	Manombo	Djletati et al., 1997, Wright (unpubl.)

<sup>1</sup> Both males and females of wild caught individuals were averaged to obtain weights in kilograms. Body mass of extinct species are estimated. Categories are based on updated IUCN Red List criteria from Mittermeier et al., 1994.

(Meier et al., 1987; Simons, 1988; Godfrey et al., 1990; Meier and Albignac, 1991; Simons et al., 1990, 1992, 1995b; Schmid and Kappeler, 1994; Zimmerman et al., 1998), as well as new information on the distribution, biogeography (Du Puy and Moat, 1996; Smith et al., 1997; Ganzhorn, 1997), physiology (Pereira 1991; 1993a,b; Schmid and Ganzhorn, 1996; Schmid, 1998), genetics (Arnaud et al., 1992; Crovella and Rumpel, 1992; Djletati et al., 1997; Rabarivola et al., 1998; Yoder et al., 1998), and behavior and ecology of previously little-studied species (Glander et al., 1989; Morland, 1991, 1993a,b; Overdorff, 1996a,b; Meyers and Wright, 1993; Sterling, 1993; 1994; Demes et al., 1995; Wright and Martin, 1995; Hemingway, 1995; Sterling and Ramarison, 1996; Warren and Crompton, 1998a,b; Kappeler, 1997b; Powzyk, 1997; Balko, 1998; Muller, 1998, 1999a,b; Fietz, 1998, 1999; Atsalis, 1997; 1999; Porter, 1998; Vasey, 1998; Mutschler, 1999. Rasmussen, 1999; Curtis and Zaramody, 1999, Tan, 1999). In addition, in both the dry forest and rain forest, long-term studies of lemur demography, life history, and reproduction (Sussman, 1991, 1992; Richard et al., 1991, 1993; Wright, 1995, 1998; Brockman and Whitten, 1996; Brockman et al., 1998; Sauther, 1998; Overdorff et al.,

1999; Jolly and Pride, 1999) have been completed in conjunction with data on tree productivity, phenology, and climate (Overdorff, 1991; Ganzhorn and Sorg, 1996; Ganzhorn, et al., 1997; Sauther, 1991; Hemingway, 1995, 1998; Powzyk, 1997; Balko, 1998; Atsalis, 1998; Ganzhorn et al., 1999a,b).

In this paper, the scene is first set by reviewing new background data on the climate, soil fertility, fruit productivity, seasonality, habitat devastation, and megafauna extinction of Madagascar. Then the evolution of lemur traits is critically examined in light of this new information. Nine traits of lemurs are examined that contrast with anthropoids and other prosimians, and the two hypotheses that have been proposed to explain the evolution of these lemur traits. The energy conservation hypothesis (ECH), emphasizes the role of the harsh island climate in selecting for these lemur adaptations, and the evolutionary disequilibrium hypothesis (EVDH) suggests that lemur traits are transitional behaviors from a nocturnal existence to a more diurnal lifestyle, allowed after the Holocene extinctions. An evaluation of the support for and against each hypothesis is given in light of recent empirical data. A more comprehensive hypothesis, the energy frugality hypothesis



Fig. 1. Map of Madagascar with sites of long-term lemur research. Number of lemur species and annual rainfall in millimeters are listed underneath sites. The indigenous vegetations types are shown. North is up.

(EFH) is suggested EFH predicts some lemur traits are a result of energy conservation, while other lemur traits maximize extraction of food resources in a harsh environment. At the end, I suggest future directions for lemur research and conservation.

#### A MADAGASCAR ENVIRONMENTAL PRIMER: THE ECOLOGICAL SETTING

In order to understand lemur ecology, it is necessary to review the new long-term data on climate and fruit productivity; as well as examine the recent new subfossil finds. The geographic location and climate of Madagascar may have had a major impact on the evolution of lemur traits. The island of Madagascar, the fourth largest island in the world, is over 1,000 km long and contains three basic habitats, all containing lemur communities: the southern, dry spiny desert habitat interspersed with gallery forests, the deciduous western tropical forests, and the eastern rain forests (Fig. 1).

Recent studies of Madagascar ecology, combined with long-term climate data suggest that a combination of long historic isolation, poor soils, and low plant productivity, in an erratic and severe climate could play a major role in lemur evolution (Ganzhorn et al., 1999). However, are the evolutionary geography and ecology of lemurs so different from those of primate species in other continental regions, that they have provided a different framework for the evolution of lemur life history and behavior? Smith and Ganzhorn (1996), in their paper contrasting lemurs and Australian marsupials, suggest that both radiations were strongly influenced by these restricting environmental factors that contrast with many tropical habitats in South America, Africa, and mainland Asia.

#### Rainfall and drought

Rainfall varies in lemur habitat, from 500 mm per year in deciduous forests of the south and west (Sorg and Rohner, 1996; Fig.



1) to 1,500 to 4,000 mm per year in eastern rain forests (Hemingway, 1995, Du Puy and Moat, 1996, Tan, 1999). Severe drought years have occurred recently in Madagascar and may be part of a cyclical pattern (Sauther, 1991, 1998; Gould, 1992; Jolly, 1998; Gould et al., 1999). In the 1991–1992 drought at the dry, western site of Beza Mahafaly, there were many months with absolutely no rain, but droughts have also been recorded in 1949, 1957, 1959, 1964, 1976, and 1982 (Gould et al., 1999). Droughts also affect the rain forest. In 1991–1992 the drought extended the rain forest dry season by 2½ months, but reduced the annual rainfall by only one-sixth of a normal year (Ranomafana National Park unpublished records). In contrast, during the 1982 drought that affected the rain forests of East Kalimantan, Indonesia for 10 months, one-third the average rainfall occurred (Leighton and Wirawan, 1986).

Drought in rain forests has resulted in high canopy tree mortality (Milton et al., 1994; Condit et al., 1995); reproductive failure, [72.7% of the sampled canopy trees in Kibale Forest, Uganda (Struhsaker, 1997)], fruit crop failure [in Panama and Borneo (Foster, 1982; Leighton and Wirawan, 1986)], and decrease in young leaf abundance [in Africa, Asia, and the Americas (Foster, 1982, Leighton and Wirawan, 1986; Struhsaker, 1997)]. What effect does drought have on tropical fauna? In South American rodents, fruit scarcity decreases the number of young born per adult female, as well as age and size of individuals at sexual maturity (Adler and Beatty, 1997). In Sri Lanka, young monkey females and infants died after severe environmental stress (Dittus, 1977, 1988). The rain forest fauna in the Americas may not respond immediately to the stress of drought (Leigh et al., 1990), but increased aggression and competition for food and water and increased infant mortality have been recorded in Malagasy dry forest lemurs during droughts (Nakamichi and Koyama, 1997; Nakamichi et al., 1996; Sauther, 1991; 1998; Gould et al., 1999).

### Cyclones and storms

The island of Madagascar, unlike Borneo or Sumatra, is within the cyclone belt (10°–

20° latitude) and the Malagasy ecosystems must endure these stochastic, abiotic disasters. Between 1920 and 1972, 362 cyclones hit the island of Madagascar, averaging seven major storms a year (Donque, 1975; Ganzhorn, 1995b). Four-fifths of these cyclones originate in the Indian Ocean, gathering power and force from the vast expanse of sea between Australia and the vulnerable coast of Madagascar.

To an ecosystem the catastrophe of a cyclone hitting directly includes complete defoliation, blowdowns of all canopy trees, landslides, and flooding (Ganzhorn, 1995b). For a lemur this can mean that neither fruits nor leaves are available for consumption until the next spring, and only crisis foods, such as epiphytes, can be eaten (Ratsimbazafy, 1999). Direct hits by cyclones from the Indian Ocean increase in frequency from south to north, and cyclones hit in the north of Madagascar almost every year. Even in the southeast cyclones once in 10 years can be disastrous. In 1997, after the worst cyclone in recorded history (275 km/hr winds for 12 hours) at Manombo Reserve on the Indian Ocean, 80% of the canopy was sheared off, with defoliation of remaining canopy trees. After this 1997 cyclone, diurnal lemur populations diminished by more than half at Manombo Reserve (H.J. Ratsimbazafy, personal communication).

El Niño events occur almost every decade (1965–1966, 1972–1973, 1982–1983, 1997–1998), and high rainfall years are usually followed by drought years (Diaz and Kiladis, 1992; Grant and Grant, 1996). The ocean current events of El Niño may derive independently from the cyclone cycles, adding additional environmental unpredictability to Madagascar.

In primate habitats with similar latitudes, such as Central America, where hurricanes can be problematic, the biogeographic history is very different. Central America's connection with South America was recent enough that no endemic primate genera have evolved, and source populations from connected forests have been available to replace those decimated by disasters. Madagascar, small in size compared to the continents, and isolated for 88 million years in its present vulnerable position in the Indian

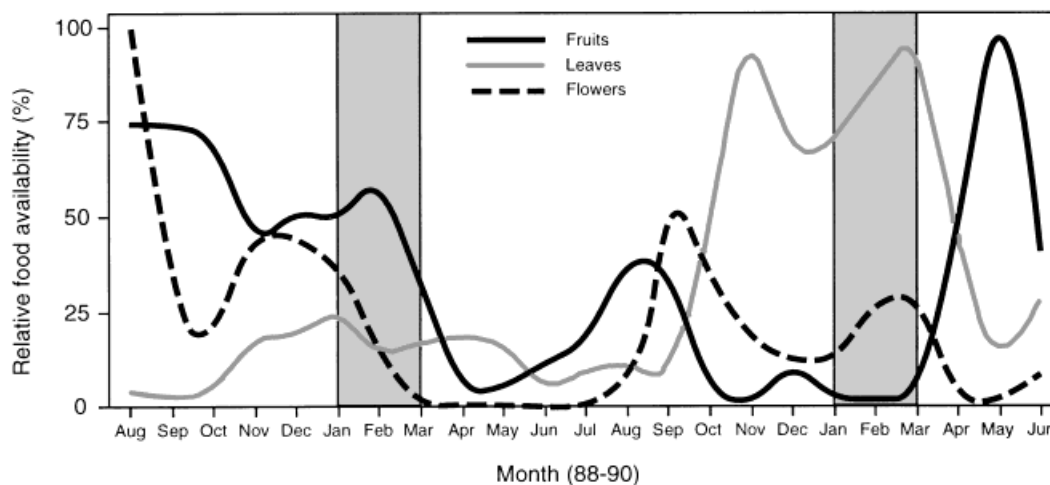


Fig. 2. Phenology of fruit, leaves, and flower availability in the rain forest of Ranomafana National Park. The period of weaning in *Propithecus* is shaded. Note the relatively low food availability for 1989 March–October, while the same period in 1988 and 1990 had at least partly more food available. The period of late lactation and weaning in *Propithecus* had high availability of fruits and flowers in 1988 and leaves in 1989. Adapted from Overdorff (1996a).

Ocean seems to have offered a special case to primates to evolve.

#### Frost and cold

Southern latitudes also can be chilled by Antarctic storms in the months of June through August, and in the Amazon 4–7 days of very cold weather may occur in July each year (Terborgh, 1983). In Madagascar, even as far north as Ranomafana National Park, vegetation has been frozen and killed by frost (P. C. Wright, personal observation). Destructive hail storms are common in Andringitra Reserve and Ranomafana at this time of year (P. C. Wright, personal observation). Lemurs rest more during cold (Morland, 1993b; Schmid and Ganzhorn, 1996; Powzyk, 1997; Schmid, 1998), but no sickness, or deaths have been attributed directly to low temperatures, although higher infant mortality of *Propithecus diadema edwardsi* occurs at this time of year (Wright, 1995).

#### Soil fertility and tree growth

Soil fertility overall in Madagascar is low, often lower than in other primate habitats on other continents (Ganzhorn et al., 1999). Madagascar eastern rain forest has acidic, extremely infertile soils, high in iron and aluminum and low in phosphorus (Johnson,

1994), while the deciduous, dry forest soils are slightly more fertile (Ganzhorn et al., 1999). In both east and western forests, tree growth is slower and fruit productivity lower than measured in sites in South America or Africa (Terborgh, 1983; Sorg and Rohner, 1996; Terborgh et al., 1997; Struhsaker, 1997; Ganzhorn et al., 1999a).

#### Seasonality in fruiting in rain forest

Despite the similarity of Madagascar in number of species and number of stems found in tropical forests of other geographic areas (Sussman and Rakotozafy, 1994; Abraham et al., 1996; Lowry et al., 1997), the fruiting patterns in Madagascar contrast with other rain forests (Wright, 1997b) (Fig. 2). Fruiting occurs throughout the year in Kibale Forest, Uganda (Struhsaker, 1997); Ketambe, Sumatra (van Schaik, 1986); Manu, Peru (Terborgh, 1983; Gentry and Terborgh, 1990); Gabon (Gautier-Hion et al., 1985); Barro Colorado Island, Panama (Foster, 1982), Manaus, Brazil (Lovejoy and Bierregaard, 1990); and Maraca, Brazil (Nunes, 1998) with a tendency for slightly lower fruit production in the driest months.

Seasonal peaks in the abundance and scarcity of foods used by lemurs are variable from year to year in Malagasy rain forests,

and many canopy species produce flowers and fruit on prolonged, irregular, asynchronous or alternate year cycles (Morland, 1991, 1993a,b; G. Schatz, personal communication; Hemingway, 1995; Powzyk, 1997).

In the rain forest at Ranomafana National Park, Overdorff (1993) studied the phenological sequence of 104 individual trees of 26 plant species representative of the forest and consumed by primates over 2 years, and found a 5-month period from March to August with almost no fruits available. Fruit was most scarce from May–June 1989, but the highest fruit availability was observed May–June, 1990 (Overdorff, 1996a) (Fig. 2). Other studies have shown this same pattern in variable annual food availability, i.e., in one year July or December will have abundant fruit while the next July or December, because of frost or cyclone damage, may have no ripe fruits (Meyers and Wright, 1993; Overdorff, 1993; 1998; Hemingway, 1996, 1998). These months of fruit scarcity can create severe constraints and necessitate definite coping strategies for obligate frugivores. This pattern of unpredictability requires lemurs to be able to adapt to energetic constraints at almost any time of the year. Many lemurs are able to survive by switching from a fruit-laden diet to leaves (Meyers and Wright, 1993), flowers (Hemingway, 1996), and hemiparasite leaves (Atsalis, 1997).

Although in other tropical rain forests, such as Kibale Forest, long-term phenology data on individual trees show that fruit production varies greatly for individual trees, there is fruit available in the forest all year (Struhsaker, 1997). And in rain forests with extended periods of fruit scarcity, such as Manu Park, keystone resources, such as figs (large-crowned) or nectar (abundant patches) provide food for frugivores (Terborgh, 1983; Wright, 1989b). Madagascar rain forests, unlike other forests with 12–14 species of sympatric primates, have a much longer period without fruits. These long periods without fruits have been proposed to have resulted in the evolution of few obligate frugivores (Fleming et al., 1987; Tattersall, 1982; 1988; Dew and Wright, 1998; Overdorff and Strait, 1998; Goodman et al., 1997),

but nonetheless fruits, seeds and flowers compose 40–80% of the annual diet of *Lemur*, *Varecia*, *Eulemur* ssp., *Propithecus*, *Microcebus*, *Cheirogaleus* and perhaps *Mirza* and *Phaner* (Overdorff, 1992, 1993, Wright and Martin, 1995; Ganzhorn and Kappeler, 1996; Hemingway, 1996, 1998; Powzyk, 1997; Balko, 1998; Overdorff and Strait, 1998; Atsalis, 1999; Ganzhorn et al., 1999b).

### Tree crown diameters in Malagasy rain forest

Another important contrast between Madagascar and Asia, South America and Africa is that crown diameters of fruit trees used by lemurs are much smaller than fruit crowns used by primates in other rain forests (Ganzhorn, 1988, 1989; Ganzhorn et al., 1999a). For example, the average crown diameter fed on by monkeys in the Manu National Park, Peru was 25 m, and at Maraca, Brazil feeding crowns ranged from 20–40 m (Terborgh, 1983, Wright, 1986, Nunes, 1998). The mean tree crown diameters (patches sizes) of fruit trees in Madagascar fed in by lemurs is 12 m in the pristine forest (Overdorff, 1996a,b; Hemingway, 1998; Balko, 1998). When looking at crown volume, the difference becomes more striking. The same number of trees with crown diameters less than half the size produce much less fruit in Madagascar, compared to more continental forests such as the Amazon and Africa (Terborgh, 1983; Clarke and Clarke, 1992; Struhsaker, 1997). The lack of large crown diameters in Madagascar may be another result of cyclone damage selecting against broad crowns, as broad crowned trees are toppled first by high winds (H.J. Ratsimbazafy, personal communication).

### Holocene extinction history

The deforestation and burning of 80% of Madagascar's original forests occurred progressively beginning about 1,600 years ago, with giant lemurs, pygmy hippos, giant tortoises, and the world's largest bird, *Aepyornis*, becoming extinct, as the fragile habitat was destroyed (Dewar, 1984; Richard and Dewar, 1991). The widespread annual burning, still engrained in the Malagasy culture,



has destroyed the seed banks and prevents restoration or recovery in many areas (Johnson, 1994). There is archeological and linguistic evidence that the initial colonization of the island, one of the last major islands colonized by humans, began around 400 AD (Dewar, 1984). Subfossil sites show extinction occurred progressively, and may still be going on today (Godfrey et al., 1997a,b; Simons, 1997). There are suggestions that giant lemurs were sighted alive in the 1600s (Simons, 1997).

**Giant Subfossil Lemurs.** Sixteen or more species of "giant" lemurs, all larger than living species, ranging in size from 11 to 200 kg, were part of the widespread mass extinction throughout most of Madagascar (Table 1) (Godfrey et al., 1997a). Subfossil lemurs are dated as early as 20,000 years ago, but most remains are dated between 1,000 and 2,000 years before present (Simons, 1997). The anatomical and dental evidence identifies giant subfossil lemurs as primarily arboreal, slow-moving folivores (Godfrey et al., 1997a). The extant lemur bones are found with the subfossils and up to 17 species of primates are found in the central plateau fossil site Ampazambazimba, an hour west of Antananarivo (Godfrey et al., 1997a). Since all the extinct lemurs are considerably larger than the 33 extant species, and probably folivores and browsers on vegetation, they might be in limited competition for food with the living lemurs, even living sympatrically (Jungers et al., 1995, 1997; Godfrey, et al. 1997a).

**Giant Subfossil Predators.** Giant subfossil predators are found in the subfossil record. The recent discovery of large raptor subfossils, including two species of *Aquila* (the size of the living American golden eagle), and *Stephanoetus* (the size of the living African martial eagle) suggest that they were large enough to prey on some of the giant subfossil lemurs (Goodman, 1994a,b; Goodman and Rakotozafy, 1995, 1997). A large mammalian carnivore, the size of a small mountain lion, also is extinct with the giant subfossil lemurs (Dewar, 1984).

### Trends in Madagascar's climate after Holocene destruction

Madagascar has undergone major habitat destruction in the last millennium, resulting in a complete loss of 80% of endemic habitat, and this deforestation has resulted in major erosion and drying of western and central habitats (Wells and Andriamihaja, 1997; Burney, 1997; MacPhee and Marx, 1997). However, there is no evidence that unpredictable and severe cyclone cycles or fruit seasonality have been modified during this time.

**Modern Community Composition.** Lemurs show precise niche differentiations, and evidence for interspecific competition (Ganzhorn, 1988, 1989, 1993; Glander et al., 1989; Overdorff, 1993, 1996a,b; Freed, 1996; Erikson et al., 1998), and their communities represent highly nested subsets on the taxonomic level in the evergreen as well as in the dry, deciduous forests (Ganzhorn, 1998). In a test of the relationship between ecologically functional groups of lemurs, Ganzhorn (1997) showed that recent habitat change has impacted species compositions of lemurs in the dry west more than the lemurs of the eastern rain forests. Ganzhorn's (1997) test of Fox's assembly rule for functional groups of lemurs emphasizes the possibility of evolutionary disequilibrium, at least in the composition of dry west and central lemur communities.

### PUZZLING LEMUR TRAITS

#### Female dominance over males

Generally in monkeys, males are dominant over females, or females and males are co-dominant (Smuts et al., 1987; Wright, 1993; Strier, 1996). However, most Malagasy lemur species organize their societies with adult females dominant over all males (Richard, 1987). Female lemurs are winners in aggressive interactions against males, and unequivocally take feeding priority, with males giving submissive vocalizations and retreating when challenged *Lemur catta* (Jolly, 1966, 1967, 1984, 1998); *Propithecus verreauxi* (Richard and Heimbuch, 1975; Richard, 1978; 1987; Kubzdela et al., 1992); *Indri indri* (Pollock, 1979; Powzyk, 1997);

*Microcebus murinus* (Perret, 1982; Pages-Feuillade, 1988); *Varecia variegata* (Kauffman, 1991; *Propithecus diadema edwardsi* (Wright, 1995); *Propithecus diadema diadema* (Powzyk, 1997); *Daubentonia madagascariensis* (Rendall, 1993); *Phaner furcifer* (Charles-Dominique, 1995); *Eulemur mongoz* (Curtis and Zaramody, 1999)]. In the rain forest indriids, adult males wait outside the fruit tree until adult females and their offspring have finished feeding and exited the tree (Pollock, 1979; Wright, 1995; Powzyk, 1997). Is this female dominance a primitive retention, or has this dominance evolved as a response to ecology (Jolly, 1984; Sauther, 1993a,b; van Schaik and Kappeler, 1993, 1996)? In prosimians from both Asia and Africa, including lorises, galagos, tarsiers, and pottos, males are dominant over females, suggesting that female dominance is not primitive in primates (Charles-Dominique, 1977; Richard, 1987). Using a protocol developed for measuring dominance patterns in *Lemur catta* on *Eulemur fulvus*, the dominance pattern is less clear-cut, with *Eulemur* males not always being submissive (Pereira et al., 1990; Pereira, 1998; Overdorff, 1998). This variation in dominance allows us to examine whether ecology may play a role in the degree of female dominance (Overdorff, 1996a).

Recent lemur research suggests that female dominance, both social dominance and feeding priority, and the corresponding male behaviors may be distributed along a continuum, more like that seen in New World monkeys (Strier, 1996). *Lemur catta* shows aggressive extremes in female dominance in male-female multiple groups (Jolly, 1966). Curtis and Zaramody (1999) documented not only female feeding priority, but "mate guarding" by *Eulemur mongoz* females. Other *Eulemur* females manifest female leadership over males with less aggression. Pereira and McGlynn (1997) following on earlier studies of *Eulemur fulvus rufus* in captivity (Vick and Pereira, 1989; Pereira et al., 1990; Pereira and Kappeler, 1997) suggest that female brown lemurs choose an alternative to female dominance by allowing a series of male companions over the course of their lifetime. Overdorff (1998), in her long-term field observations of brown le-

murs, showed quantitatively that the proximity of these male partners actually increased fruit feeding rates for females, perhaps lowering the need for vigilance by the females.

But is there any indication of male dominance in any lemur species? In New World monkeys, male dominance occurs when males can monopolize access to resources, such as male *Cebus* monkeys opening tough palm nut clusters (Janson 1992, Strier, 1996). Most food resources in Madagascar are in small packets and obtained by scramble competition (vine leaves) or intragroup contest competition (fruits) that do not require large size or strong teeth for extraction. However, if there is a monopolizable resource requiring special abilities of males for extraction, male dominance would be predicted to occur in Madagascar, providing the opposite pole for the dominance "continuum" (Strier, 1996). To date, no male dominance, where all males are dominant over all females, as seen in Old World monkeys has been described in lemurs.

A female's reproductive success depends largely on her ability to obtain enough resources to support herself and her offspring (Hrdy, 1981). Pregnancy and lactation are time-consuming and energetically expensive for all mammal mothers (Clutton-Brock et al., 1982; Clutton-Brock et al., 1983; Oftedal, 1984; Resnick, 1985). The question debated is whether gestation, lactation, and pregnancy impose relatively more energetic constraints on female lemurs than on most other mammals, necessitating female precedence and feeding priority (Jolly, 1984; Richard, 1987; Young et al., 1990). Lemur female feeding competition with males may be so costly energetically that female dominance is ritualized into an integral part of the daily routine of most lemurs throughout the year (Sauther, 1991; 1993a; Rasamimanana and Rafidinarivo, 1993). Males are charged, cuffed, and bitten if they feed where females disapprove (Jolly, 1966; Richard, 1978). Monkey mothers are also energetically stressed, and yet often males are dominant (Altmann, 1980; Altmann and Samuels, 1992). It has been suggested that pregnant and lactating lemur females may be under more or differ-

ent environmental stresses than monkeys (Young et al., 1990).

#### **Female-female competition and targeted aggression**

Some monkey species solve the problem of feeding competition with clear-cut dominance relationships among females (van Noordwijk and van Schaik, 1987; Sterck and Steenbeek, 1997). High rank females obtain greater access to preferred, limited, or clumped foods, or are able to feed more efficiently than low rank females (Isbell, 1991; Whitten, 1984). A similar pattern of dominance, although rare in prosimians, is seen in some lemurs. Aggression over food is minimized in some lemurs by dominance relationships in females with clear-cut, year-round, long-term hierarchies as seen in *Lemur catta* (Jolly, 1966; Pereira 1993a; Pereira and Kappeler, 1997). Female hierarchies often are only seasonally obvious in *Propithecus* ssp. (Richard et al., 1991; Wright, 1995; Brockman and Whitten, 1996; Powzyk, 1997) and not obvious in *Eulemur fulvus* (Sussman, 1972; Pereira et al., 1990; Pereira and Kappeler, 1997; Pereira and McGlynn, 1997; Overdorff 1998), and *Varecia* (Morland, 1993a; Balko, 1998; Vasey, 1998).

However, competition among some lemur females escalates during periods of reproductive stress and this "targeted and unrelenting aggression" by some females over other female group members overrides hierarchies. Competition and targeted aggression among female lemurs can be especially severe in the dry tropical forests of the south where *Lemur catta* live (Sauther, 1991; Koyoma, 1991; Jolly, 1998; Hood and Jolly, 1995; Sauther, 1998) resulting in females of high rank having higher reproductive success (Taylor, 1986). During the months before and during mating, as well as the birth season, eruptions of full-scale "targeted aggression" in large groups of ring-tails begin with attacking in many female pairs, and escalate to high levels of relentless aggression as attacks become concentrated on one or two female adversaries (Taylor and Sussman, 1985; Taylor, 1986; Koyoma, 1992; Pereira and Kappeler, 1997). But "targeted aggression" is by no means limited to *Lemur catta*. Lemur female-female aggression can

escalate until the targeted female is evicted from the group in *Eulemur fulvus*, *Varecia*, and *Propithecus* (Vick and Pereira, 1989; Pereira 1993a; Overdorff 1998, Wright, 1995, E. Balko, personal communication). This aggression until eviction from a group by female against female during the birth season is not documented for other primates. Female-female aggression is also seen in intergroup encounters in many lemur species, including *Propithecus diadema edwardsi* (Wright, 1995), *Haplemur aureus* (Tan, personal communication), and *Eulemur mongoz* (Curtis and Zaramody, 1999).

#### **Lack of sexual dimorphism in solitary and group living polygynous social systems**

In general, primate males with larger body weights and longer and broader canines are effective fighters in the competition over females (Clutton-Brock et al., 1977; Clutton-Brock, 1985). The fact that sexual dimorphism is greater in most monkey and ape species with more than one male mating, than in monogamous species indicates that intrasexual selection is a likely cause of size differences in male and female primates. But lemurs have all mating systems, except for harems or leks (Table 3) and the minimal body size and canine size differences between the sexes in polygynous lemurs contrasts with many anthropoid primates (Kappeler, 1991; 1993, 1996a,b, 1997 a,b; Pereira and Kappeler, 1997).

Sexual dimorphism is a composite of male features and female features, each responding to sexual selection (Kay et al., 1988; Plavcan and van Schaik, 1992, 1997). In lemurs, male-male aggression and fights can be severe, but so can female-female aggression, and indeed males are not larger in canine size and body size than females, regardless of social system (Kappeler, 1991, 1997a, but see Kappeler, 1997b). Female lemurs have proportionally larger canines than anthropoids of the same size (Kay et al., 1988), and female lemurs use these canine weapons in aggression against both males and other females (Vick and Pereira, 1989; Pereira and Kappeler, 1997). Lemurs, having seasonal bouts of both male-male aggression and female-female aggression, have same-sized canines correlating with

TABLE 3. Social groupings of lemurs according to field studies<sup>1</sup>

Genus and species	Reference
Monogamous family groups (Group size: 2–6)	
<i>Indri indri</i>	Pollock, 1979; Powzyk, 1997
<i>Cheirogaleus medius</i>	Muller, 1998, 1999; Fietz, in press
<i>Avahi laniger</i>	Harcourt, 1991; Ganzhorn et al., 1985; Roth, 1997
<i>Eulemur rubriventer</i>	Overdorff, 1996a, b
<i>Hapalemur griseus</i>	Wright, 1986; Overdorff et al., 1997
<i>Hapalemur aureus</i>	Wright, 1987, 1992; Tan, 1999
<i>Phaner furcifer</i>	Charles-Dominique et al., 1980
<i>Eulemur mongoz</i>	Tattersall & Sussman, 1976; Curtis, 1997; Rasmussen, 1999
<i>Lepilemur ruficaudatus</i> (?)	Ganzhorn and Kappeler, 1996
Multimale–multifemale fused groups (Group size: 2–27)	
<i>Eulemur albocollaris</i>	Wright, unpublished data
<i>Eulemur coronatus</i>	Freed, 1996
<i>Eulemur fulvus fulvus</i>	Rasmussen, 1999
<i>Eulemur fulvus rufus</i>	Sussman, 1972; Overdorff, 1998
<i>Eulemur fulvus sanfordi</i>	Freed, 1996
<i>Eulemur macaco</i>	Colquhoun, 1993; Andrews and Birkenshaw, 1998
<i>Hapalemur simus</i>	Wright, 1992; Tan, 1999
<i>Hapalemur griseus</i>	Grassi, unpublished data; Tan, 1999
<i>Hapalemur griseus alaotrensis</i>	Mutschler and Feistner, 1995; Mutschler, 1999
<i>Lemur catta</i>	Jolly, 1966; Jolly et al., 1993; Sauther, 1991
<i>Propithecus verreauxi</i>	Richard, 1978; Brockman and Whitten, 1996
<i>Propithecus tattersalli</i>	Meyers, 1993
<i>Propithecus diadema diadema</i>	Powzyk, 1997
<i>Propithecus diadema edwardsi</i>	Wright, 1995; Hemingway, 1995
<i>Propithecus diadema perrieri</i>	Mayor and Lehman, 1999
Multimale–multifemale fission fusion groups (Group size: 2–32)	
<i>Varecia variegata variegata</i>	Morland, 1990, 1991; Balko, 1998
<i>Varecia variegata rubra</i>	Rigamonti, 1993; Vasey, 1998
Polygynous scramble competition (solitary foragers nonbreeding season)	
<i>Daubentonia madagascariensis</i>	Sterling, 1993
<i>Mirza coquereli</i>	Kappeler, 1997
<i>Microcebus rufus</i>	Atsalis, 1998
<i>Microcebus murinus</i>	Schmid, 1999
<i>Microcebus cf. myoxinus</i>	Schwab, (in press)
<i>Lepilemur leucopus</i>	Nash, 1998
<i>Lepilemur microdon</i>	Porter, 1998
<i>Lepilemur mustelinus</i>	Ganzhorn, 1992

<sup>1</sup> One-quarter of the lemur taxa studied are monogamous, while monogamy occurs in only 3% of mammals species and 13% of anthropoid species (Kleiman, 1977).

this more or less equal intrasexual competition (Plavcan and van Schaik, 1992).

Another explanation is the “wimpy male hypothesis” (Richard, 1992) suggesting that lemur females and males have the same body mass because females choose compliant males. Small males will not challenge females and infants for food (Jolly, 1984). In addition, lemur males may be equally ineffective in predator detection and protection as females, and an increase of even double the male body size would not offer better protection for females and offspring (Wright, 1998).

#### Abundance of monogamy

Monogamy is a rare social system in mammals and occurs in 3% of mammals and in 13% of anthropoid primates (Kleiman, 1977;

Kinzey 1987). However, more than a quarter of the lemur species have been described as one breeding pair, monogamous groups (Fietz, in press; Table 3). Several hypotheses have been proposed to explain the evolution of monogamy, including that it is a (1) a primitive condition from which other social systems evolved (Eisenberg, 1977; Eisenberg et al., 1972); (2) a derived system, evolving only in special ecological conditions when valuable resources are scarce and uniformly dispensed (Wittenberger and Tilson, 1980); (3) a strategy to involve males in offspring care and increase survival of offspring (Kleiman, 1977); and (4) an anti-infanticide strategy (van Schaik and Dunbar, 1990; Palombit 1999). The high percent of monogamous lemur species, in compari-



son to other primates and mammals suggests these species may be a model to understanding the evolution of monogamy.

### **Sperm competition plus male-male aggression**

In multimale, multifemale groups where females mate with several males during a given estrous period, sexual selection favors sperm competition (Harcourt et al., 1981; Harvey and Harcourt, 1984). In some species of monkeys and apes, sperm competition may replace severe male-male aggression [tamarins (Terborgh and Goldizen, 1985); bonobos (Thompson-Handler et al., 1984); chimpanzees (Harvey and Harcourt, 1984; Krebs and Davies, 1997); woolly spider monkeys (Strier, 1994, 1996, 1997)]. In contrast, lemurs have sperm competition accompanied by intense male-male aggression during the breeding season, often resulting in long canine gashes and severe injuries (Pereira and Weiss, 1991; Sauther, 1991; Jolly et al., 1993; Morland, 1993a; Sterling, 1993, 1994; Wright, 1995; Kappeler, 1997a,b). Non-monogamous lemurs have large testes relative to their body size during the breeding season (Kappeler, 1997a,b). Sperm competition and intense male-male competition are combined with female choice, as well as lack of sexual dimorphism (Pereira and Weiss, 1991). Outside the breeding season, lemur testicles are reduced, even in polygynous species (Glander et al., 1992; Kappeler, 1997a,b). Two or three months before the seasonally breeding females come into estrus, male testicles begin to enlarge and continue to grow in volume until reaching maximum size as the females reach estrus (Pereira, 1991, 1993b; Kappeler, 1997a,b). Having the capacity to produce large quantities of sperm enables a male to inseminate many females and also have a higher chance of producing the sperm that reaches the egg in each of those females (Harvey and Harcourt, 1984). Although males of all lemur species, even monogamous species, have seasonal testicular increases, the extreme case is the gray mouse lemur, who was found in the breeding season in the wild to have testicles as large as his brain (Schmid and Kappeler, 1998).

Copulation plugs are common in some species of lemurs, including *Lemur catta* and *Microcebus* (Dixson, 1995). This compact, waxy mass of coagulated semen may form an impenetrable block to further copulations, giving the first male that reaches the female a decided advantage. The race to reach a female first during her few hours of estrus has high stakes, and the genetic evidence verifies that the male who is first to copulate may be the father of the offspring (Pereira and Weiss, 1991). One prediction is that large testicles allow maximum sperm production for copulation plugs, while male-male aggression is a competition for first in line.

### **High infant mortality, including infanticide**

There is some evidence that in lemurs that give birth to singletons infant mortality may be twice as great as that in anthropoids (Table 4). The lemurs that bear litters of two or three may lose two out of three offspring; an equivalent loss documented in the tamarins and marmosets in South America (Balko, 1998; Goldizen et al., 1996). All females must make a tradeoff between the number of offspring they produce and the quality of care that they provide (Trivers, 1972). The lemur females, like other primate mothers, may vary characteristics such as neonate birth weight, milk quality, female age at first birth, length of interbirth intervals, birth rates, and in some species litter number (Altmann, 1980; Ross, 1991, 1992, 1998; Lee et al., 1991; Tilden, 1995; Lee, 1997; Garber and Leigh, 1997) depending on environmental and social conditions. In captivity, where food is not limiting, mothers produce their first offspring at an earlier age, have higher weight neonates, and shorter interbirth intervals, compared to mothers in the wild (Small and Smith, 1986; Ross, 1998; Lee, 1997; Fedigan and Rose, 1995; Muller, 1999b). This suggests a mother's nutritional state impacts strongly on reproduction. Although large data sets are lacking from primate studies to quantify a habitat quality dependent "sliding scale of life history variation," comparisons of captive versus wild populations suggest that food availability could impact heavily on variation of life history traits, such as life-



TABLE 4. Infant mortality (% of infants that died before one year of age) in monkeys, lemurs and small apes<sup>1</sup>

Species	Body mass (kg)	Site (years)	Groups (N)	% Infant mortality	Reference
<i>Cebus olivaceus</i>	2.8	Pecuario Masaguaral (11) Venezuela	2	18.2–21.6	O'Brien and Robinson, 1993
<i>Macaca fascicularis</i>	5.4	Ketambe (7) Sumatra	2	20	van Noordwijk et al., 1993
<i>Alouatta seniculus</i>	6.7	Hato Masaguaral (11) Venezuela	2	18–21	Crockett and Pope, 1993
<i>Ateles chamek</i>	7.0	Manu (4) Peru	2	33	MacFarland-Symington, 1988
<i>Eulemur fulvus rufus</i>	2.1	Ranomafana (9) Madagascar	2	41	Overdorff et al., 1999
<i>Lemur catta</i>	2.6	Beza Mahafaly (3) Madagascar	9	30–52	Sussman, 1992
<i>Propithecus verreauxi</i>	3.5	Beza Mahafaly (5) Madagascar	27	53–70	Richard et al., 1991
<i>Propithecus diadema</i>	5.8	Ranomafana (13) Madagascar	3	55	Wright, 1995; unpublished data
<i>Hylobates lar</i>	4.4–7.6	Khao Yai (18) Thailand	8	2.3	Brockelman et al., 1999
<i>Hylobates agilis</i>	5.5–6.4	West Kalimantan (8) Indonesia	10	4.8	Mitani, 1990

<sup>1</sup> Data from long-term studies. Body weight data are from Rowe (1996). Rain forest sites (*Macaca fascicularis*, *Ateles chamek*, *Eulemur fulvus rufus*, *Hylobates lar*, *H. agilis*, and *Propithecus diadema*) and dry forest sites (*Cebus olivaceus*, *Alouatta seniculus*, *Lemur catta*, and *Propithecus verreauxi*) have been selected.

time reproductive output (Rhine et al., 1988). Infant survivorship in wild primates depends on a variety of factors, including condition of mother, care given, and random events such as predator attacks, infanticide, cyclones, and droughts (Dittus, 1977, 1988; Wright, 1995; 1998; Goldizen et al., 1988, 1996; Gould *et al.*, 1999). Data on the effect of predation on infant and juvenile primate populations suggest that death by predators may be as great or greater in Madagascar as in other regions (Cheney and Wrangham, 1987; Boinski, 1989; Janson and van Schaik, 1993; Goodman et al., 1993; Wright, 1998). More long-term data from carefully observed primate populations are needed.

Malagasy lemurs are best compared with New World primates because of the smaller body size and greater arboreality. Large lemurs, like large atelids, have single births every second or third year, while small lemurs, like the small-bodied callithricids give birth to litters of two or three offspring each year (Wright, 1990, 1997b; Ross, 1998; Strier and Zeigler, 1997).

In some species, infant mortality can be a result of infanticide (Hrady, 1979; Hrady et al., 1995). Sexual selection theory predicts that infanticide will evolve in a species if males gain a reproductive advantage. For example, the reproductive success in langurs

of an individual male is increased if he immigrates into a new group, kills nursing infants, which consequently brings the females into estrus, shortening the interbirth interval, offering an opportunity for the immigrant male to father offspring immediately (Hrady, 1979). Infanticide would not be predicted to occur in lemurs for three reasons: (1) Strict seasonal breeding precludes the possibility of a female coming into estrus after an infant is killed, and therefore infanticidal males would not gain an immediate reproductive advantage (Erhart and Overdorff, 1998). (2) In two-thirds of the species, females regularly mate with a number of males both within and outside the group, often exhibiting female choice, precluding males from having exclusive access, and not offering a male a reproductive advantage by infant killing (Sauther and Sussman, 1993). (3) More than one-quarter of the species are monogamous, and monogamy has been proposed as a viable strategy against infanticide (van Schaik and Dunbar, 1990). Indeed, infanticide has not been documented in any monogamous lemur species.

"Classic" infanticide by immigrant males has been described in some species of lemurs (Hood, 1994; Wright, 1995; Erhart and Overdorff, 1998). In a rain forest population of *Propithecus diadema edwardsi*, 23 infants

were born to the nine adult females in the 12 years of studying three groups, and of the seven infants that died under 3 months of age, five died after a takeover by an immigrant male or female (P.C. Wright, unpublished data). Three infanticides were observed, and two inferred (Wright, 1995). One infanticidal male was rejected and ousted from the group by the females within 2 months. However, the second infanticidal male was accepted by the two breeding females, and may be the father of two offspring born a year after the infanticides. And the third suspected infanticidal male also stayed in the group and bred. At another Ranomafana rain forest site 5 km away, another "classic" infanticide in *P. d. edwardsi* was observed after an immigrant male arrived in the group (Erhart and Overdorff, 1998). This immigrant male remained in the group and may have bred the following year. Using sexual selection theory, a prediction may be made that infanticide by immigrant males would only be seen in species such as *Propithecus* who usually give birth in alternate years (Van Schaik and Kappeler, 1993). Although females do not come into estrus immediately, they will come into estrus 1 year earlier than a nursing mother. Immigrant infanticidal behavior would be expected in the species with slower growing infants such as *Propithecus diadema edwardsi* (Tan and Wright, 1994), but not in smaller species with fast growing infants and annual interbirth intervals (Pereira, 1993b). Indeed, in long-term field studies of *Eulemur fulvus rufus* infanticidal males have never been observed (Overdorff, 1998).

### Cathemerality

Except for one anthropoid primate, *Aotus azarae*, all primates not living on the island of Madagascar have either a strict nocturnal or diurnal activity cycle (Wright, 1989b; 1994). Sussman and Tattersall (1976) first described the abilities of lemurs to be able to alternate activity between day and night, when they described the normally diurnal *Eulemur mongoz* sipping flower nectar from *Ceiba pentandra* flowers at night. Overdorff (1988) documented day and night time activity of *Eulemur rubriventer* in her 24-hour

observations in the rain forest, and found that 6 hours of activity during the night was balanced by sleeping 6 hours during midday. All the species within the genus *Eulemur* have now been described as having an activity cycle that involves both day and night activity including feeding (Sussman and Tattersall, 1976; Tattersall, 1988; Overdorff, 1988; Overdorff and Rasmussen, 1995; Colquhoun, 1998; Curtis and Zaramody, 1999; Rasmussen, 1999). This type of lifestyle, including both nocturnal and diurnal behavior, has been defined by Tattersall (1988) as cathemerality. In addition to *Eulemur*, there is evidence that *Hapalemur simus*, *Varecia variegata variegata*, and *Hapalemur griseus alaotrensis* exhibit cathemeral behavior (Mutschler, 1999; L. Balko, personal communication; C. Tan, personal communication). But *Lemur catta* (Jolly, 1966; Sauther, 1991), *Hapalemur griseus griseus* (Wright, 1989a; Overdorff et al., 1997), *Propithecus* spp. and *Indri indri* (Richard, 1978; Wright, 1995; Kubzda, 1997; Powzyk, 1997) are strictly diurnal, whereas *Cheirogaleus* (Wright and Martin, 1995; Muller, 1999; Fietz, 1999), *Daubentonia* (Sterling, 1993), *Microcebus* (Atsalis, 1998; in press a,b; Schmid, 1998), *Phaner* (Charles Dominique, 1995), *Avahi* (Roth, 1997; but see Warren, 1997), *Lepilemur* (Ganzhorn, 1989, 1993; Porter, 1998; Nash, 1998) and *Mirza* (Kappeler, 1997b) are strictly nocturnal.

### Low metabolic rate and torpor

Most nocturnal primates have low metabolic rates (Muller, 1985; Muller et al., 1985; McNab and Wright, 1987; Wright, 1989b), but both diurnal and nocturnal lemurs studied have low metabolic rates (Daniels, 1984; Richard and Nicoll, 1987; Schmid and Ganzhorn, 1996; Schmid, 1998). The small-bodied lemurs may even have daily torpor (Schmid, 1998) or 4–6 months of hibernation (Wright and Martin, 1995; Fietz, 1998).

### Photoperiod and restricted breeding

In general, seasonal breeding is not unusual, especially in temperate environments. The strategy of breeding early in the spring so that offspring can be self-sufficient by fall is well known (Lack, 1964), but the

timing of breeding in the tropics is usually more flexible due to less seasonality of food resources. However, in the tropical environment of Madagascar, we find an unusual situation where each species of lemur has strict breeding seasonality, with a limited period of estrus for each female each year, triggered by daily sunlight totals (photoperiodicity) entrained in the pituitary gland (van Horn and Resko 1977; Petter-Rousseaux, 1980). This limited estrus is so firmly entrenched that lemurs transported to different latitudes change their breeding days according to local light levels (Rasmussen, 1985). Breeding for each species is more or less synchronized within groups and between groups in a 1 or 2 week period (Sauter, 1991; Richard, 1974; Pereira, 1991, 1998; Wright, 1995). The time that a female lemur is in estrus is short, only 4–32 hours [Jolly, 1966; Richard, 1974; Foerg, 1982a,b; Sauter, 1991; Morland, 1993a; Wright, 1995; but see Brockman and Whitten (1996) for variability found in *Propithecus*]. In all the cheirogaleids, aye-aye, and *Varecia* females, vaginas are normally sealed shut, and only open during estrus (Foerg 1982a,b; Feistner and Taylor, 1998; Fietz, 1998). The male's increases in testicle size are synchronized with the female's estrus and vaginal opening (Foerg, 1982a, b; Morland, 1993a; Pereira, 1993b). Testicles are small for most of the year, with annual testicular development beginning 3 months prior to the female's estrus cycle (Glander et al., 1992; Pereira and Weiss, 1991; Pereira 1993b; Kappeler 1997a). These factors restrict mating by either males or females outside of the mating season. In addition to visual cues of labial swelling and reddening in *Propithecus*, *Eulemur*, *Lemur*, and *Varecia*, lemurs have excellent olfactory abilities and chemical signals communicate sexual readiness and sexual stage (Foerg, 1982a,b).

Hormone levels, testicular size, and body weights fluctuate seasonally in monkeys, such as *Saimiri* and *Macaca* (Shideler, et al., 1993). However, in contrast to lemurs, almost all neotropical African and Asian primates can breed at any time of year even if they are transported to other latitudes, and the breeding peaks seen in the wild disappear in captivity (Altmann, 1980; Hrdy,

1981). Although African and Asian prosimians have birth peaks in the wild, these birth periods are over 4–6 months, not a few weeks, and breeding can occur at any season in captivity. The breeding seasonality of lemurs which is restricted to a few hours a year, and photoperiod dependent even when transported to the Northern Hemisphere, is unique in primates (van Horn and Resko, 1977; Rasmussen, 1985).

## TWO HYPOTHESES ON EVOLUTION OF LEMUR TRAITS

Building on the new data on climate, phenology, and subfossils, several possible hypotheses have been developed to explain some of the lemur traits that contrast lemurs with anthropoids. In this section, I will briefly outline two of these hypotheses, the energy conservation hypothesis (ECH) and the evolutionary disequilibrium hypothesis (EVDH), and examine the nine targeted lemur traits in light of predictions derived from these two hypotheses (Table 5).

### The energy conservation hypothesis (ECH)

Looking for ecological correlates of behavioral differences among primates from different continents has been useful to understanding the effects of ecology (Terborgh and van Schaik, 1987; van Schaik et al., 1993; Chapman et al., 1995; Kappeler and Heyman, 1996). The ECH in a broad sense incorporates an ecological approach to understanding lemur traits, comparing differences in Madagascar environment with other continents. The ECH, first proposed by Jolly to explain the evolution of female dominance in lemurs, suggests that Madagascar ecology and environmental challenges including strong seasonality have led to energetic stress, especially on reproductively active lemur females (Jolly, 1966, 1984; Richard, 1987; Young et al., 1990; Wright, 1993). According to the ECH, female lemurs have responded to the reproductive stress created by a harsh ecology with female priority in feeding situations (Jolly, 1984; Young et al., 1990). Pereira (1993a,b) and Sauter (1993a, 1998) expanded this hypothesis to suggest that the harsh, but predictable seasonality of nutritive resources has led lemurs to

TABLE 5. Nine lemur traits that differ from most other primates and the limits explained by ECH and EVDH<sup>1</sup>

Trait	ECH	EVDH	Reference <sup>2</sup>
Female dominance	xx	?	1–8, 10
Female targeted aggression	xx	xx	5, 13, 14
Lack of sexual dimorphism	xx	?	9, 13
Abundance of monogamy	xx	?	10, 13, 15
Sperm competition + male aggression	?	?	13
High infant mortality	?	?	10
Cathemerality	?	xx	12, 13, 16, 17
Low BMR, hibernation and torpor	xx	?	6, 13
Photoperiod and estrous synchrony	xx		8, 11

<sup>1</sup> The energy conservation hypothesis (ECH) proposes that Madagascar's unique ecological pressures and limited food resources have selected for female dominance and in a broader interpretation other lemur traits. The evolutionary disequilibrium hypothesis (EVDH) suggests that the Recent megafaunal extinctions, especially the large raptors, have influenced lemur traits. Selected references address the issues.

<sup>2</sup> References: 1. Pollock, 1979; 2. Jolly, 1984; 3. Richard, 1987; 4. Pollock, 1989; 5. Vick and Pereira, 1989; 6. Young et al., 1990; 7. Pereira et al., 1990; 8. Sauther, 1991, 1993; 9. Richard, 1992; 10. Wright, 1993, 1995; 11. Pereira, 1993a, b; 12. Overdorff and Rasmussen, 1995; 13. van Schaik and Kappeler, 1996; 14. Pereira and Kappeler, 1997; 15. Jolly, 1998; 16. Tattersall, 1987; 17. Rasmussen, 1999.

evolve life histories comprehensively geared toward the conservation of energy. The energetic stress of the Malagasy winter season is suggested to have favored the evolution of a set of photoperiodically regulated traits in these primates, including seasonal energy storage, strict seasonal reproduction, modulation of metabolic rate, growth rate, temperature regulation, fat deposition, activity level, and timing of aggressive behavior peaks (Pereira, 1993a,b).

#### Evolutionary disequilibrium hypothesis (EVDH)

The EVDH was developed to explain the evolution of traits that show lack of convergence between gregarious lemurs and anthropoids (van Schaik and Kappeler, 1996). EVDH suggests that the large-scale ecological changes accompanying the deforestation, aridification, and erosion seen within the last millennium and a half, resulting in the extinction of the large diurnal raptors (Goodman, 1994a; Goodman and Rakotozafy, 1995, 1997), and the loss of 16 species of large-bodied lemurs (Godfrey et al., 1997a) have “produced a mismatch between current activity patterns and adaptations to activity period influencing social cohesion, estrous synchrony, mating behavior” (van Schaik and Kappeler, 1996). This EVDH offers an historical approach and novel insights into evolution of lemur behavior. Previous studies of fossil assemblages (for example, of the Pleistocene extinctions) indicate that extinctions influence the evolution of new commu-

nities, by individual species responding to the environmental changes differently in accordance with their own tolerance limits, causing the expansion of population sizes and geographic ranges of some species (Graham and Lundelius, 1984). The mega-subfossil extinctions of Madagascar occurred recently, and offer an opportunity to observe post-extinction recovery. In the fossil record, post-extinction recovery patterns are a “complex tapestry, woven by surviving lineages, the expansion of opportunists, innovation and diversification of new lineages” (Erwin, 1998, p 344).

The EVDH argument for Madagascar hinges on the possibility that adaptations to diurnal lifestyle evolved recently, within the last 500–1,000 years, after the extinction of the large raptors *Aquila* and *Stephanoetus* (Goodman, 1994a,b) released the larger lemurs from fearing predation by the diurnal birds. “Since large raptors were present in Madagascar into the Holocene, this suggests that all arboreal lemurs of the size range surviving today were largely nocturnal before this period” (van Schaik and Kappeler, 1996). Cathemeral species are proposed as nocturnal species in transition from the recent nocturnal ancestor. One of the lynch pins of this hypotheses is that social systems of non-nocturnal lemurs are groups formed by species “adapted to live in pairs” (van Schaik and Kappeler, 1996). One of the results of this ancient monogamy may be small group size of living lemurs today. The EVDH suggests very rapid (within 100–150



generations of large lemurs) changes in behavior influencing social structure of populations of many species with primarily one change in predator extinction.

## EVOLUTION OF LEMUR TRAITS: ECH VS. EVDH

### Female dominance (male-female competition)

**ECH.** One prediction derived from the ECH is that if food is continually a scarce resource in this energy-poor environment, females will take feeding priority over males to be able to have enough food to raise offspring successfully. Jolly (1984), building on earlier observations (Jolly, 1966; Richard, 1978; Pollock, 1979), proposed that lemur females take feeding priority over males because of the high energetic requirements of reproducing in an environment with limited food. At first the high energetic stress imposed on gestating lemur females, because of their low metabolic rates compared to monkeys, was emphasized (Richard and Nicoll, 1987; Young et al., 1990), and then, the high energetic stress of lactating and weaning mothers was targeted (Sauther, 1991, 1993a, 1998; Meyers and Wright, 1993). The ECH predicted that gestating and lactating females would take feeding priority more often than nonreproductive females and males. In studies of *Lemur catta*, this prediction was supported as lactating females ate more and had more aggressive interactions over food (Rasamimanana and Rafidinarivo, 1993; Sauther, 1993a). However this is not a true test of this hypothesis, since it is clear that gestation and lactation are costly to all female primates and mammals, and it is still unclear why feeding priority evolved in lemurs, and not the other taxa.

The ECH also predicts that in the more seasonal, southern dry forests where *Lemur catta* is found, the feeding competition would be more severe than in less seasonal habitat. Indeed, *Lemur catta* females have a higher rate of aggression toward males than *Eulemur fulvus rufus* females (Pereira and Kappler, 1997). In the dry forest species, *Propithecus verreauxi* females have a higher rate of aggression towards males (1–3×/10hours) (Kubzdela et al., 1992; Richard, 1985) than the rain forest *Propithecus diadema ed-*

*wardsi* (0.1–0.3×/10hours) (P.C. Wright, unpublished data). The prediction that energy is a less scarce resource in the rain forests of Madagascar is supported by data from both *Propithecus diadema edwardsi* in Ranomafana and in the larger-bodied *Propithecus diadema diadema* or *Indri indri* at Mantady where females ate more than males, but no significant differences were found in feeding amounts of gestating, lactating, or cycling females (Tan and Wright, 1995; Powzyk, 1997). Future research should focus on more lemur species and comparisons of feeding between males and females, lactating, gestating, or cycling. ECH would predict that species found in the spiny desert and those that go into torpor would have more female dominance and aggression, especially during the period of lactation (Pereira 1993a,b; Sauther, 1998).

An alternative explanation for the high rates of aggression in dry forest lemurs is that the soils of the west are more fertile, and the productivity of trees are higher on an annual cycle and more consistently productive year after year than the eastern rain forest trees. Accordingly, the diversity of lemur taxa is lower and population densities of lemurs are higher, resulting in more aggression (Ganzhorn et al., 1999a).

As predicted by the ECH, during the drought period at Beza Mahafaly, adult female mortality was 20.8% with most of the females lactating at time of death (Gould et al., 1999). Richard (1992) suggested that female choice to mate with same-sized, compliant males and refusal to mate with larger, more aggressive males enabled female dominance to continue. The ECH hypothesis would predict that the “wimpy male” traits would continue in the population especially if during environmental crisis of droughts or cyclones, the larger males were selected out. Unfortunately, this prediction has not yet been tested since, when males disappear, they cannot be followed and they could either emigrate or die (Gould et al., 1999).

The ECH would predict that if lemur females were under such high energetic stress, that a system would evolve where all females have feeding priority in order for these females to produce more energy-rich



milk than monkeys to speed infant growth. This prediction was supported by Pereira's (1993a,b) study of growth and weight gain in *Lemur catta* infant and juvenile lemurs, as infant weight gain was high before the season of scarce resources, and much higher than observed for any anthropoid primate.

Although an early analysis of *Lemur catta* milk had partially supported the ECH prediction that lemur milk would be energy-rich, the sample size was small (Buss et al., 1976). However, Tilden and Oftedal's (1995, 1997) more rigorous analysis of 12 species of prosimians, revealed that all lemur milk is not alike, and all *Eulemur* species (*E. fulvus*, *E. macaco*, *E. mongoz*, and *E. rubriventer*) produce dilute, low-protein, low-fat milk. Tilden and Oftedal (1997) suggested that species, such as *Lemur catta*, *Eulemur* spp., and *Propithecus*, that are continually carried by the mother, have constant access to the nipple, and may suckle large quantities of dilute milk. However, high-energy milk coupled with a short lactation period duration and fast infant growth was found for lemurs producing litters. The milk of *Varecia* and *Cheirogaleus* were energy rich with *Varecia* milks high in lipids and protein (Tilden and Oftedal, 1997).

Field and captive studies give new support for the ECH predictions that conservation of energy could have been a selective force in the evolution of female dominance in lemurs. Aggression of females over males is more frequent and intense in *Lemur catta*, the species in the most seasonal and driest habitat than other lemurs with populations farther north (Pereira and Kappeler, 1997). Pereira in his captive work on *Lemur catta* had shown that maximal growth rates of infants are sustained for the first 6 months of life, declining at the autumnal equinox, the beginning of the scarce resource season in Madagascar. These experiments in captivity showed that regardless of food availability the provisioned lemurs' growth was controlled by photoperiodicity (Pereira 1993b). This implies a long evolutionary history of fine-tuning between lemur reproduction and environmental cues. Future research examining differences in growth trajectories in species other than *Lemur catta* would further test this relationship between fast infant growth and female dominance.

**EVDH.** According to the EVDH, female dominance in all lemurs is a retention from the "ancestral monogamous lemurs" (van Schaik and Kappeler, 1996), as the living members of ancestral primate lineages are nocturnal. One assumption from the EVDH might be that female dominance would exist in other nocturnal primates. But there is no female dominance reported in galagos, lorises, pottos, or tarsiers (Charles-Dominique, 1977; Bearder, 1987; Gursky, 1998). A second assumption made from the EVDH is that there is female dominance in non-Malagasy monogamous primates. In monogamous primates not from Madagascar, usually there is co-dominance, with females often leading to food trees (Wright, 1984; 1993; Kappeler, 1993b; Palombit, 1994, 1995).

Female dominance has been documented in both nocturnal and diurnal lemurs (Kaufman, 1991; Kubzdela et al., 1992; Rendall, 1993; Charles-Dominique, 1995; Fornasieri and Roeder, 1993), and the original reasons for the evolution of female dominance in the "ancestral monogamous nocturnal lemurs," (van Schaik and Kappeler, 1996) remain unclear.

#### Targeted aggression and female-female competition

**ECH.** If conservation of energy is the prime force for evolution of behavior, and the most energetically stressful time for females is lactation, it is predicted that more female-female competition and aggression will occur during lactation. This ECH prediction is supported as targeted aggression in *Eulemur fulvus*, *Lemur catta*, *Varecia variegata*, and *Propithecus diadema edwardsi* and is concentrated after the birth season, during lactation (Taylor, 1986; Vick and Pereira, 1989; Sauther, 1993a; Wright, 1995; Pereira and Kappeler, 1997; Overdorff et al., 1999).

**EVDH.** The EVDH suggests that female-female targeted aggression is a retention of female competition from monogamous ancestors. It is predicted that this intensified female aggression would not be observed in nocturnal lemurs, since nocturnal lemur females are widely dispersed in separate territories in monogamous or solitary social

systems. To my knowledge, female-female aggression in nocturnal lemurs has not been studied.

"Mate-guarding" is an important component of the female-female aggression observed in monogamous primates (Kleiman, 1977; Wright, 1984; Mitani 1984, 1985; Palombit, 1994a,b, 1999; Reichard, 1995). Another prediction from the EVDH is that female-female aggression would increase during the mating season, as retention of monogamous "mate-guarding" behavior. This is supported by observations of female-female aggression in *Lemur catta* during the breeding season (Taylor, 1986; Pereira and Kappeler, 1997), and "mate guarding by females" in monogamous *Eulemur mongoz* in the wild (Curtis and Zaramody, 1999). Future field research might examine female-female aggression during the breeding season in other species.

#### Patterns of sexual dimorphism

**ECH.** One prediction from the ECH is that lemurs are not sexually dimorphic because males are as large as is energetically possible. It is well known that large males eat more and cost more to nursing mothers (Clutton-Brock *et al.*, 1982). If females in species with high sexual dimorphism have sons, often they forfeit the next birth season in order to recover (Clutton-Brock *et al.*, 1983). In addition, if food is scarce especially over long periods of time, larger males could take feeding priority and deplete resources that females may need to survive and have successful offspring. It is possible that these large, aggressive males were selected out by not being able to eat enough during droughts and cyclones and only smaller-bodied, more energetically efficient lemurs survived to breed in the next generations.

Another prediction based on the conservation of energy is that lack of sexual dimorphism may be part of a system to keep the males subordinate. Females gain control by a combination of estrus synchrony, seasonal breeding restricted to a few hours or a day and female choice of compliant males (Pereira and Weiss, 1991; Sauther, 1991; Richard, 1992; Sauther and Sussman, 1993). Females may be big with large canines as a result of female-female competition (Play-

can and van Schaik, 1997), but males may not be bigger, because of female choice (Small, 1989).

But recent evidence from an elegant study in the deciduous dry forest of the gray mouse lemur (Schmid and Kappeler, 1998), with supporting data from the rain forest rufous mouse lemur (Atsalis, 1999) show that males gain body mass before and during the breeding season, as has been seen in South and Central American squirrel monkeys (Boinski, 1987), and previously reported for *Lemur catta* in captivity (Pereira, 1993a,b). This energetically efficient method of dealing with seasonal male-male competition by seasonal sexual dimorphism in body mass could support the ECH hypothesis. Perhaps this is a trend in other polygynous species of lemur, and future research should include monitoring male body mass in the field.

**EVDH.** It is predicted that the lack of sexual dimorphism seen in living lemurs is a retention from the nocturnal, monogamous social system in species of lemurs before the extinctions of large raptors occurred (van Schaik and Kappeler, 1996). Excluding Madagascar, both diurnal and nocturnal monogamous primates are not sexually dimorphic, and polygynous nocturnal primates are sexually dimorphic (Clutton-Brock and Harvey, 1977). This prediction implies that sexual dimorphism has not evolved yet, in these species which are behaving polygynously. This raises interesting questions about differences in the rate of morphological changes and behavioral changes. There is no evidence that the "transition" polygynous males are becoming larger, since they have been released from "nocturnal monogamy." Although polygynous lemur females are more tolerant toward their adult female offspring than monogamous females, there is evidence that they are aggressive toward nonrelated females in their groups (Taylor and Sussman, 1985; Vick and Pereira, 1989; Pereira and Kappeler, 1997).

Other evidence does not support this prediction. The large subfossil lemurs also are not sexually dimorphic, suggesting that the same evolutionary processes selected for same-sized males and females in all lemurs (Godfrey *et al.*, 1997a). Several species of

nocturnal lemurs, including *Microcebus* ssp. and *Lepilemur* ssp. are not monogamous, nor are they sexually dimorphic (Kappeler, 1996).

#### Abundance of monogamous social systems

**ECH.** In many ways, monogamy can be ranked as a highly energy-efficient social system in a nutritionally stressful environment. If patch sizes (fruit tree crowns) are small all year, but relatively uniformly spaced, living in small groups within small territories may be the best tactic (Emlen and Oring, 1977; Wright, 1986). Large groups may require ranging more widely to find food and/or mates and an increase in energy expenditure (Sterling, 1993; Janson and Goldsmith, 1995). The sparse distribution of small resources in Madagascar would fit monogamous social structure, since females are too widely spaced for males to defend more than one (Emlen and Oring, 1977; Clutton-Brock and Harvey, 1977). One prediction is that to conserve energy lemurs would live in small groups to take advantage of small tree crowns, and lower fruit productivity. This is supported by the following: As lemur group size increases, intragroup competition over access to food increases (Hood and Jolly 1995; Rasamimanana and Rafidinarivo 1993, Sauther, 1991; Wright, 1995). Harem groups, which are hypothesized to be prevalent if breeding females can live together on abundant or clumped resources (Wrangham, 1980; Andelmann, 1986; Altmann, 1990; Sterck et al., 1997), do not exist in Madagascar's lemurs, perhaps because resource patch size is never big enough.

**EVDH.** The EVDH suggests that lemurs have retained monogamy from their recently nocturnal ancestors. If monogamy is considered a social structure evolving from solitary to polygynous, the EVDH prediction may be supported. However, in most mammals, including primates, monogamy is rare and considered a derived condition (Kleiman, 1977). Except on the island of Madagascar, a strictly monogamous social system is seen only in the primates *Aotus*, *Callicebus*, and most species of *Hylobates* (Wright, 1986; Tilson, 1981). The sole primate example of

monogamy evolving into polygamy is the callithricids, which evolved a polyandrous social system, perhaps in reaction to heavy predation (Terborgh and Goldizen, 1985; Sussman and Garber, 1987). To date there are no polyandrous lemurs described.

The EVDH arguments seem contrary to theories of the evolution of sociality, which describe the advantage of having more eyes and ears to detect predators and the dilution effect against predators overriding the disadvantages of food competition and parasite increases incurred by sociality (Alexander, 1974; van Schaik and van Hoof, 1983; Terborgh and Janson, 1986; Janson, 1992; Cote and Poulin, 1995; Janson and Goldsmith, 1995). According to social behavior theory, release from predation pressure might push lemurs to become more solitary to avoid feeding competition (van Schaik 1983), and yet there is no evidence of that trend, and no diurnal lemurs are solitary. The relationship between monogamy and recent raptor extinctions is not strongly supported.

#### Sperm competition and male-male aggression

**ECH.** Considering energy conservation, sperm competition should be energetically less expensive than aggressive male-male competition for access to females. This may be a less energy-depleting way for males to compete for mating success by producing large quantities of sperm during the breeding season, relying on sperm competition, rather than maintaining a larger body mass year-round to successfully fight other males for reproductive access (Harcourt et al., 1981). Indeed, *Lemur catta*, *Propithecus diadema edwardsi* and *Varecia variegata*, *Daubentonia*, *Microcebus* and *Mirza coquereli* males increase testicular size to up to five times before the breeding season (Pereira, 1993b; Perret, 1982; Glander et al., 1992; Morland, 1993a; Feistner and Taylor, 1998; Kappeler 1997a,b; Powzyk, 1997; Glander and Powzyk, 1998; Fietz, 1998; Atsalis, 1999; Balko, 1998). Since sperm production involves some cost to males, monogamous males may do better to guard their partners for those 10–12 hours a year when they are sexually receptive, than by producing large quantities of sperm (Harvey and Harcourt,

1984). The monogamous lemur males thus far caught in the wild (*Hapalemur aureus*, *Avahi laniger*, *Eulemur rubriventer*, *E. mongoz*, *Indri indri*) have significantly smaller testicular volumes than males from sympatric multimale, multifemale breeding groups, even when seasonal differences are controlled (Glander et al., 1992; Glander and Powzyk, 1998; Curtis and Zaramody, 1998).

But this ECH prediction is only partially supported by the data. Sperm competition in polygynous lemurs is not as "low energy" as seen in some New World primates (Milton, 1985; Strier, 1992, 1996, 1997), as male lemurs chase and attack each other during the breeding season (Jolly, 1966; Richard, 1974; Sauther, 1991; Sterling, 1993; Morland 1993a; Wright, 1995; Kappeler, 1997a). Although males may conserve energy all year, they expend energy and perhaps risk their lives for breeding opportunities for that 1 or 2 days.

**EVDH.** Predictions derived from the EVDH would suggest that the nocturnal, monogamous ancestor would have small testes, as found in monogamous primates. Monogamous lemurs do have smaller testes compared to solitary or multimale, multifemale groups, as predicted by sexual selection theory (Glander et al., 1992; Dixon, 1995; Kappeler, 1997a). The seasonally enlarged testes of both nocturnal and diurnal polygynous prosimians reflect the occurrence of sexual selection via sperm competition in 72% of the extant species (Dixon, 1995; Sterling, 1993; Kappeler, 1997a,b; Schmid and Kappeler, 1998). There is a contradiction in the EVDH that sperm competition and polygyny are recent phenomena restricted to diurnal lemurs, evolving within several hundreds of years since the subfossil extinctions, as most species of nocturnal lemurs are also polygynous with males having very large testes during the breeding season (Sterling, 1993; Kappeler, 1997b; Schmid and Kappeler, 1998).

#### High infant mortality and infanticide

**ECH.** Lemurs living in an unpredictable, harsh climate may opt for a strategy of low investment in infants (Wright, 1995), or high investment for only a short period of

time (Pereira, 1993a,b). This is supported by the high infant mortality (40–80%) seen in populations studied over 10 years (Sussman, 1991, 1992; Richard et al., 1991, 1993; Wright, 1995, 1998; Overdorff et al., 1999; Gould et al., 1999; Jolly and Pride, 1999). This contrasts with long-term studies of monkey populations with infant mortality about half of the lemur rates (Crockett and Rudran, 1987a,b; Crockett and Pope, 1993) and long-term ape studies which report very few infant deaths, especially in gibbons (Goodall, 1986; Leighton, 1987; Palombit, 1999). The high infant mortality of lemurs may be expected from a group where one-third of the species have litters of 2–5 offspring, a strategy usually reserved for small mammals and birds that lose many offspring randomly to predation (Bartlett et al., 1993). Also, lemur infants have lower birth weights than monkeys of the same adult size (Benirschke and Miller, 1981; Wright, 1990; Rasmussen and Tan, 1992). For example, the 6-kg *Propithecus* mother gives birth to a newborn about the same weight as the 1-kg *Aotus* or *Callicebus* (Garber and Leigh, 1997).

From our limited knowledge of some lemur species, growth trajectories for lemurs seem to fall into two groups. *Lemur catta*, with the southernmost and coldest, driest habitat have infants that grow quickly to reach a large enough body mass to withstand the rigors of winter (Pereira, 1993a,b). Smaller-bodied infant lemurs with the harsh deadline before the cold, resourceless winter grow even faster to reach adult body mass before April (Benirschke and Miller, 1981; Foerg, 1982). For example, in the rain forest the small-bodied *Cheirogaleus* and *Microcebus* infants are born in December and reach nearly adult size within 4 months to have enough fat reserves to withstand torpor (Wright and Martin, 1995; Atsalis, 1998). In contrast, infants of the large-bodied group, including *Propithecus* and *Indri*, which are on a slower schedule with birth intervals for females of 2 years or more, grow proportionally slower than small-bodied lemurs (Richard et al., 1991, 1993; Wright, 1995; Powzyk, 1997). Infant *Propithecus diadema* weigh only 135–155 g at birth, 20% of adult body weight at 6 months, less than half (43%)



adult body weight at 1 year (Glander et al. 1992; Hemingway, 1995; Powzyk, 1997) and 58% of adult body weight at 2 years, reaching 78–90% adult body weight at 3 years of age in the wild (P.C. Wright, unpublished data). Extrapolating from weights of wild individuals at different ages, *Propithecus diadema* infants gain 5.5 g/day for the first 6 months of life while receiving mother's milk (one-thousandth of mother's weight per day) but then gain weight nearly twice as fast (at the rate of 9 g/day, a 600th of mother's weight per day) for the second 6 months during weaning (N = 6; P.C. Wright, unpublished data).

A correlation is predicted between infant weight gain and milk composition with richer milk being produced in the faster growing species. As discussed earlier, compared to monkeys and apes, some lemurs including *Eulemur* spp., *Lemur catta* and *Hapalemur griseus* have dilute, low-energy milk, while the milk quality of a *Varecia* and *Microcebus* was richer, especially in lipids and protein (Myher et al., 1994; Tilden and Oftedal, 1997). Early studies of *Lemur catta* milk composition (Buss et al., 1976) suggested that fast growth by *L. catta* may not be just higher quality milk, but also greater rate of milk delivery. Indeed infant lemurs that cling to mothers, rather than are parked, have continuous access to the nipple, and continual suckling is possible (Tilden and Oftedal, 1997). It should be noted that these lemur statistics are contrasting with recent evidence that anthropoid folivores have faster growth rates (Leigh, 1998) and that milk in anthropoid folivores is higher in protein content.

Low quality milk and small infant birth weights give support to the possible strategy of lowered investment per lemur offspring because of density independent mortality. Increased maternal investment (higher quality of milk or increased length of lactation) is unlikely to greatly decrease probability of mortality from predation, infanticide, or cyclones. Thus there may be selection pressure for a mother to keep some resources in reserve, so that a mother will be in sufficient good health to produce an infant at the next cycle (Wright, 1995).

Infanticide, like predation, is only observed opportunistically and data accrue only after many years of research. One prediction derived from the ECH is that if competition for scarce resources drives female behavior: females killing other female's infants will occur more often in the most seasonal habitat, and in the species with the largest groups.

This prediction is only partially supported by the current data. Although *Lemur catta* lives in large groups in an extremely seasonal habitat in the south of Madagascar, *Eulemur macaco* lives in a more tropical habitat in northern forests (Hood, 1994; Andrews, 1998). Female infanticide was observed in both species when group size was increasing and food competition was high.

**EVDH.** One prediction derived from the EVDH is that mortality due to predation, including infant mortality, might be low, after release from predation by large, now extinct, raptors. However, as field data shows, infant mortality is high in all lemur populations studied (Richard et al., 1991; Sussman, 1991; Wright, 1995, 1998; Overdorff et al. 1999; Gould et al., 1999; Atsalis, 1999, Jolly and Pride, 1999). Also predation on lemur populations is high, with the main predators including extant raptors, the extant mammalian carnivores (*Cryptoprocta ferox*, the fossa, and *Galidea elegans*, the ring-tailed mongoose), and the Malagasy boa (Goodman et al., 1993; Rasoloarison et al., 1995; Wright and Martin, 1995; Wright, 1998, Rakotondravony, et al., 1998; Karpanty and Goodman, in press). This is obviously difficult to test, but some predation rates on anthropoid populations are lower than known lemur rates (Cheney and Wrangham, 1987; Janson and van Schaik, 1993.)

### Cathemerality

**ECH.** Engqvist and Richard (1991) proposed that cathemerality was a strategy by four species of "cathemeral" lemurs (*Eulemur fulvus rufus*, *E. f. mayottensis*, *E. mongoz*, and *E. rubriventer*) to feed on leaves and flowers at night during the dry season, when fruits are not available. However, a nutritional analysis showed that leaves have increased carbohydrates late in the after-



noon (Ganzhorn and Wright 1994), which might encourage nocturnal lemurs to begin feeding late in the afternoon, which they have not been observed to do (Harcourt, 1991; Roth, 1997; Porter, 1998; Nash, 1998; Rasmussen, 1999). Also, in the cold, dry season a strategy to conserve energy might be to sunbathe, rest huddle, as seen in *Lemur catta*, *Indri indri*, *Propithecus* ssp., *Varecia variegata*, and *Lepilemur* (Jolly, 1966; Richard, 1978; Powzyk, 1997; Morland, 1993b; Nash, 1998).

If cathemeral behavior is a strategy to maximize intake of low quality food, it would be predicted that nocturnal behavior might increase during periods of fruit scarcity, to allow more time to find food. This was tested in three *Eulemur* species (Overdorff and Rasmussen, 1995; Colquhoun, 1993, 1998; Curtis and Zaramody, 1999; Rasmussen, 1999), and seasonal differences in activity related to feeding were not found.

Moonlight could be a positive factor in encouraging night activity because of increased visual acuity, but the evidence is equivocal. Black lemurs were night active year-round during the waxing moon and full moon, suggesting that high light levels are used in seeing and communicating as documented in nocturnal primates not afraid of predators (Charles-Dominique et al., 1980; Nash, 1986; Wright, 1989b; Andrews and Birkenshaw, 1998; Colquhoun, 1998). This behavior is directly the opposite that is observed in most nocturnal mammals who avoid bright moonlight to avoid predation (Morrison 1978; Wolfe and Summerlin, 1989; Emmons et al., 1989; Julien-Laferriere, 1997). But this pattern is not found in all eulemurs, since nocturnal light levels had no significant effect on activity levels or nightly path length for *Eulemur mongoz* or *Eulemur fulvus fulvus* at Ampijoroa (Rasmussen, 1999).

Rasmussen (1999) suggests three different ecological influences on cathemerality: (1) total shift from day activity (wet season) to night activity (dry season) (*Eulemur mongoz*) partially to take advantage of nocturnally available nectar resources and partially to avoid raptors; (2) seasonal shift from day activity to 24 hour activity (western populations of *E. fulvus* to avoid expo-

sure to raptors in a leafless winter forest); (3) 24 hour activity year round (*Hapalemur griseus aloatrensis*, rain forest *Eulemur fulvus rufus*, *Eulemur rubriventer*), perhaps to avoid human predators (*H. g. aloatrensis*) or interference competition (rain forest eulemurs). It should be noted that during the day all lemurs use low energy behavioral modifications including crypticity, resting, maintaining small group size, sleeping low in trees in the day, and high in trees in the night as a dual strategy to both conserve energy and avoid predators (Wright, 1998).

**EVDH.** Because of the historical nature of this hypothesis, there is no way to directly test this prediction, but there are empirical data that suggest that the EVDH, as the ECH, may not totally explain cathemerality.

1. Nocturnal lemurs (*Avahi*, *Cheirogaleus*, and *Microcebus*) frequently are eaten by diurnal hawks and eagles during the day while they are sleeping (Goodman et al., 1993; Wright and Martin, 1995; Wright, 1995, 1998; Overdorff 1996; Balko, 1998; Karpanty and Goodman, in press). The extinct and extant eagles could have eaten the "supposedly then nocturnal" *Propithecus*, *Indri*, *Lemur*, *Eulemur*, *Varecia*, *Hapalemur* during the day when they were sleeping as well.
2. In addition, the nocturnal aye-aye is similar in body size to *Varecia*, and larger than *Eulemur* and *Lemur*, but has not become diurnal after the large raptors went extinct.
3. Deaths of *Propithecus diadema edwardsi* by fossa have been at night, usually in the dark of the moon, when the victim is asleep (Wright et al., 1997; Wright, 1998). *Propithecus* have not changed their activity pattern to be alert during the night when this major predator is active.

The EVDH predicts that lemur aerial predator alarm calls evolved to warn against the large, now extinct, raptors (Goodman, 1994) Observations of wild lemurs cast doubt on this prediction. *Indri indri*, *Propithecus diadema diadema*, and *Propithecus diadema edwardsi*, the largest living lemurs, give aerial alarm calls and drop low in the trees after an extant hawk or eagle is sighted

(Powzyk, 1997; Wright, 1998). This same behavior is seen in the cathemeral and diurnal medium sized lemurs (Macedonia 1990; 1993; Sauther, 1989, 1993b; Gould, 1996; Gould et al., 1997; Colquhoun, 1998, C. Tan, personal communication). If these lemurs have become diurnal only recently, then the call would also have to have evolved recently.

Human hunters do not have flashlights in Madagascar, and hunt during the day with slingshots, and very rarely, guns. It is therefore interesting that in areas where hunting by humans exists, there is no evidence of *Propithecus* or *Indri* becoming nocturnal (Meyers, 1993; Powzyk, 1997; C. Welch, personal communication). Archeological evidence suggests that human hunters replaced the extinct giant raptors as predators during the same time period (400–1500 years ago) (Dewar, 1984; 1997), and selection pressure to avoid diurnal predators would continue.

The EVDH prediction that the larger lemurs became diurnal within the last millennium does not take into account their folivorous diet. The lack of nocturnality in *Propithecus* and *Indri* has been proposed to be due to their specialization to feed on young leaves which have distinct coloration (Pollock, 1979; Powzyk, 1997) and thus cannot be easily selected in the dark. [It should be noted that all lemurs tested are able to discriminate colors (Jacobs and Deegan, 1993)]. In contrast, the cathemeral *Eulemur* has a more generalized diet which may require less visual cues. In addition, nutrition of leaves is high in the afternoon (Ganzhorn and Wright, 1994) which would further compromise night leaf feeding. It thus seems that the EVDH would predict a large range of evolutionary changes (e.g., strict diurnality and selective folivory) in the ecology of few lemur species during the last 400–1,500 years. In the case of *Propithecus* or *Indri* this time may equal less than 150 generations.

It is possible that humans hunted to extinction the large hawks and eagles (*Aquila* and *Stephanoetus*), as well as their prey, the giant subfossil lemurs. In fact, the subfossil evidence suggests that the major prey item of the giant raptors might have been some of

the smaller giant lemurs (under 20 kg), since they were the largest prey items available (Goodman 1994a,b; Simons, 1997). One extreme interpretation of the EVDH is that the giant subfossil lemurs would have all been nocturnal to avoid the large raptors (or humans). Paleontologists have equivocated, based on eye socket size, that giant lemurs could have been diurnal, nocturnal or both (Tattersall, 1982; Ross, 1995).

The fact that all lemurs have a tapetum lucidum, a light reflecting shield behind the retina, that allows lemurs to see well in the dark gives support for the EVDH (Pariente, 1980). However, *Eulemur fulvus* and *E. mongoz*, cathemeral lemurs, have a poorly developed partial tapetum, while *Lemur catta* and *Propithecus*, diurnal lemurs, have intact tapetums. Thus, the *L. catta* and *Propithecus* would be better candidates for nocturnality in the past.

#### Low BMR, torpor, and hibernation

**ECH.** According to the ECH, lemurs “shut down” metabolism to conserve energy. This prediction has been supported by quantitative field data on low metabolic rate, torpor, and high quantities of resting by lemurs, especially during the season of scarce resources (Ganzhorn, 1993; Wright and Martin, 1995; Morland, 1993; Nash, 1998; Schmid and Ganzhorn, 1996; Schmid, 1998). *Cheirogaleus* spp. go into hibernation for 4–6 months every year (Petter, et al., 1977; Wright and Martin, 1995; Muller, 1998), and *Microcebus* also enter torpor for several days at a time (Ortmann et al., 1997; Fietz, 1998; Schmid, 1998; Atsalis, 1999). *Lepilemur ruficaudatus* has the lowest basal metabolic rate recorded for any folivorous mammal (Schmid and Ganzhorn, 1996). This adaptation of lowering BMR, torporing, and/or hibernating to conserve energy is found among both frugivorous and folivorous lemurs and is effective both against extreme cold and scarce foods.

**EVDH.** The EVDH predicts that low basal metabolic rate is a retention from the nocturnal ancestor. All nocturnal primates have low basal metabolic rates (Muller, 1985; Muller et al., 1985; McNab and Wright, 1987; Wright, 1994), and few diurnal anthro-

poids have low basal metabolic rate (Davies and Oates, 1994).

### Photoperiod and restricted breeding

**ECH.** Does strict reproductive seasonality save energy for lemurs? Birth peaks during food abundance provide a selective advantage to the lactating mother of having abundant resources available (Hrdy, 1981; Goldizen et al., 1988, 1996). Infants that have a head start on life, grow bigger faster, have a reproductive advantage later (Clutton-Brock et al., 1982). Therefore for the medium-sized and small lemurs this breeding seasonality may be an advantage (Sauther, 1991; 1998; Pereira, 1993a,b). However, this explanation appears to not hold for the large-bodied lemurs, such as *Propithecus* and *Indri*, that give birth before the cold winter season in Madagascar (Richard, 1978; Wright, 1995; Powzyk, 1997). These infants must survive 3–5 months of scarce resources, and seasonal breeding does not appear at first to be advantageous for these larger species. Is there a better explanation that includes lemurs of all sizes?

Synchronous breeding may be advantageous for female control of males, and female control of males (dominance) allows female feeding priority throughout the year (Paul, 1997). The number of females simultaneously in estrus strongly affects a male's capacity to monopolize all females, and therefore constrains the exclusivity of the mating access (Berenstein and Wade, 1983; Ridley, 1986). Alpha males are unable to monopolize conceptions when two or more females are in estrus simultaneously (Altmann, 1990). From the female's point of view, breeding synchrony combined with promiscuity is an effective tactic to confuse paternity, thereby decreasing the chances that their infants will be victims of male infanticide (Altmann, 1990; Paul, 1997). The reproductive success of high ranking males may be more severely constrained by breeding seasonality than by the number of male rivals (Bulger, 1993; Paul, 1997). The field narrows even more if estrus is restricted to 4–32 hour periods for individuals (Evans and Goy, 1968; Richard, 1974; Sauther, 1991; Sterling, 1993; Wright, 1995) with a species mating season as short

as 5 days to 2 weeks (Jolly, 1966; Sauther, 1991, Overdorff, 1998).

Females within *Lemur catta* groups come into estrus a day or two apart, giving the older females a few days advantage to attract all the males nearby (Pereira, 1991, 1998; Pereira and Weiss, 1991) and all the group's females (usually close relatives) the advantage of restricting the males from traveling to other groups for copulations. In a field study of fecal hormones of *Propithecus verreauxi*, there was variation in timing of estrus among females in the population (Brockman and Whitten, 1996), suggesting a wider window of estrus behavior than thought previously. Future research should test whether this pattern is true for other lemur species.

However, in addition to explanations of female energetics and female control of males, another possible advantage to mothers of synchronizing births with others of the same group might be predator satiation. If there are abundant infants in the forest, the predator may choose to eat someone else's offspring (Boinski, 1989).

**Synchronized weaning, not synchronized births.** Studies of dry forest living *Lemur catta* have suggested that lemur life histories, including synchronous births, are comprehensively geared for the conservation of energy, in order to withstand the harsh seasonality of the environment and its scarce resources (Sauther, 1991, 1998; Pereira 1993a,b). In contrast to trends seen in most primate communities in the neotropics, Africa, or Asia (Terborgh, 1983, Struhsaker, 1997, Gautier et al., 1985; Chapman et al., 1999), primate species in Madagascar rain forests do not have birth peaks. In Madagascar sympatric species may give birth at very different months, varying from May–June (*Propithecus diadema*) to December (*Microcebus rufus*).

As long-term data accumulated from Rano-mafana National Park on life histories of the sympatric species, it became clear that individuals within a species were synchronized in births, but that different species gave birth at different times of year (Fig. 3). This is very different from the typical spring breeding seen in the temperate zone so that

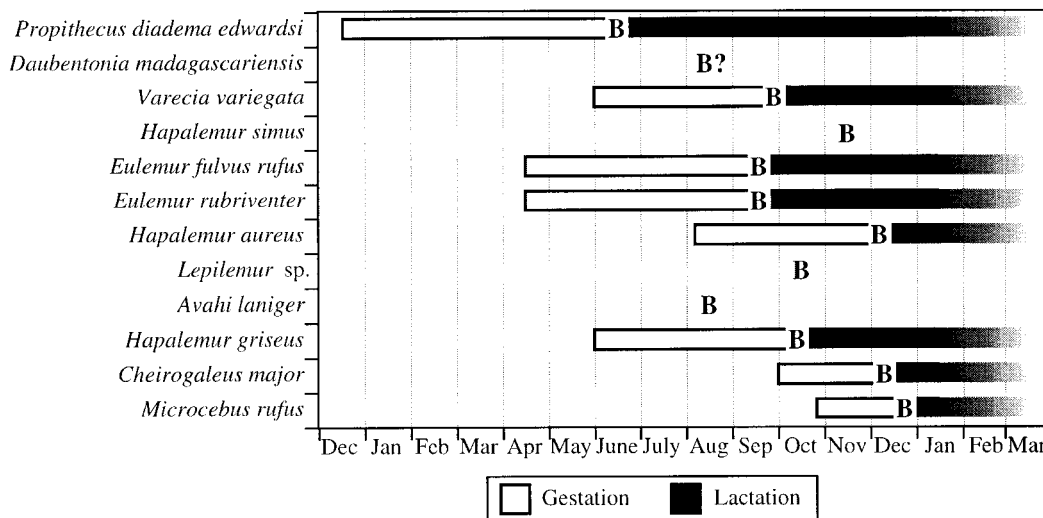


Fig. 3. Life history annual schedules for 11 of 12 species of the sympatric lemur community at Ranomafana National Park in Madagascar. B denotes births. Weaning occurs around the end of March in all studied species. Note birth asynchrony and weaning synchrony in these rain forest species.

infants can be fledged or weaned by the long, cold winter. Over a 13-year period, field studies of nine of the species of sympatric lemurs conducted in Ranomafana National Park in southeastern Madagascar rainforest have documented this aseasonality of species births (Harcourt, 1991, Roth, 1997; Atsalis, 1997; Balko, 1998; Overdorff, 1996a,b; Overdorff et al., 1999; Merenlender, 1993; Hemingway, 1994; Wright and Martin, 1995; Wright, 1992, 1995; Tan, 1999). Life history events, including copulations, births, and weaning, were observed in eight species and births and weanings in an additional three species (Fig. 3). Behavioral observations of infants and mothers were used to document duration of lactational dependence and age of weaning. In primates, facultative suckling often continues up until the next birth of an infant, and weaning may be considered a process over a long time span (Nicholson, 1987). I defined weaning as the age at the end of the period of primary dependence on the mother for nutrition when independent foraging away from the mother makes a major contribution to the offspring's energy intake (Lee *et al.*, 1991). Weaning marks a nutritional transition, when the infant becomes a juvenile and is more vulnerable to the risks of malnutrition, infection, and pre-

dation (Janson and van Schaik, 1993; Kuzawa, 1998).

Comparisons of life history variables of the Ranomafana rain forest lemurs show that adult body masses range from 42 to 6,300 g, and gestation and lactation vary according to body size. Results show that births ranged over a 6-month period for the nine species studied, but all species weaned offspring by late March (Fig. 3). With fruit abundance unpredictable, January through March are the most certain months that food, including leaves and insects, will be available (Figs. 2 and 4).

As discussed at the beginning of this article, peak fruit production in the Malagasy rain forest is 3 months shorter on average and unpredictable compared to peak fruit production in the Amazon forest (Terborgh, 1983; Wright, 1997b), and the African forest (Gautier-Hion et al., 1985; Struhsaker, 1997). Insect abundance and the appearance of abundant new leaves are more restricted in Madagascar, while spread over 9–12 months in other tropical forests (van Schaik, 1986; Terborgh and van Schaik, 1987; van Schaik et al., 1993; Oates, 1994; Sauther, 1993; Meyers and Wright, 1993; Hemingway, 1995, 1996, 1998; Wright, 1996; Ganzhorn and Sorg, 1996; Overdorff, 1996a,b;



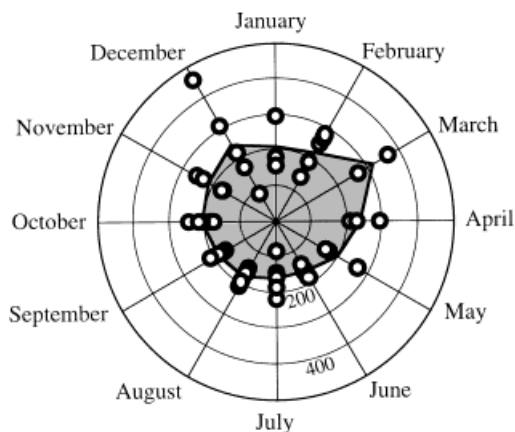


Fig. 4. Composite feeding minutes of two groups of *Propithecus diadema edwardsi* over a 9-year period (1987–1996). Data from Ranomafana National Park, Talataky Trail System Groups I and II. Each black circle represents a year's monthly average for individual's feeding minutes. The line encircling the dark shading is the mean of years. Note how *Propithecus* consistently eat less during June–October, and the increase in variance and average fruit feeding between November–May.

Atsalis, 1997; Struhsaker, 1997; Ganzhorn et al., 1999a).

Because food abundances are squeezed into a narrow time frame, it is not possible for larger-bodied lemurs to lactate, wean, and gestate in the period of those 3 months. In each of the larger rain forest species, the choice appears to be to breed in the warm, wet months, give birth during the cold, sparse resource months, lactate when resource abundance is low and wean the offspring at the time when chances are highest for most foods to be available. With this strategy, the infant has time to gain weight for the period of scarce resources ahead (Pereira, 1993a,b), and the female has time to build up her reserves for producing the next offspring. Although weaning at a time when high quality and abundant foods are available has been shown in other mammals, cueing in to optimum weaning time appears to be a priority in lemur life histories. Thus the lemur strategy is to synchronize the weaning, not gestation, births, or early lactation, with possible food abundance.

**EVDH.** The EVDH does not address the restricted breeding season within species in all lemurs.

## CONCLUSIONS

Over the past decade and a half, field studies of lemurs have increased greatly as Madagascar has become more accessible to research. In this paper, I have organized the new information around nine lemur life history and behavioral traits that contrast with anthropoids in order to focus on possible differences in selective pressures in Madagascar. Two main hypotheses, the energy conservation hypotheses (ECH) and the evolutionary disequilibrium hypothesis (EVDH) have been suggested as partial explanations for lemur behavioral traits including female dominance, lack of sexual dimorphism in polygynous primates, both sperm competition and male-male competition in males, cathemerality, torpor and hibernation, strict seasonal breeding entrained by photoperiods (Table 5). I examined these hypotheses in light of long-term Madagascar climate, botanical phenology and fruit productivity data, and recent information from the wild on life history schedules.

There is no single explanation that covers the evolution of all nine lemur life history traits. A broad interpretation of the ECH, based on a combination of environmental and ecological constraints of the island of Madagascar, seems to help explain many of the lemur life history variables. However, all of the lemur traits do not strictly conserve energy, but some also maximize the extraction of scarce resources. Thus, it is perhaps more appropriate to reconsider ECH as an "energy frugality" hypothesis (EFH) and postulate that the majority of lemur traits are either adaptations to conserve energy (e.g., low BMR, torpor, sperm competition, small group size, seasonal breeding) or to maximize use of scarce resources (e.g., cathemerality, territoriality, female dominance, fibrous diet, weaning synchrony) (Fig. 5).

The abundance of monogamy and small group size (Table 3) of lemurs may be attributed to the smaller crown diameters and nonproductivity of the trees in Madagascar compared to other continental areas (Ganz-



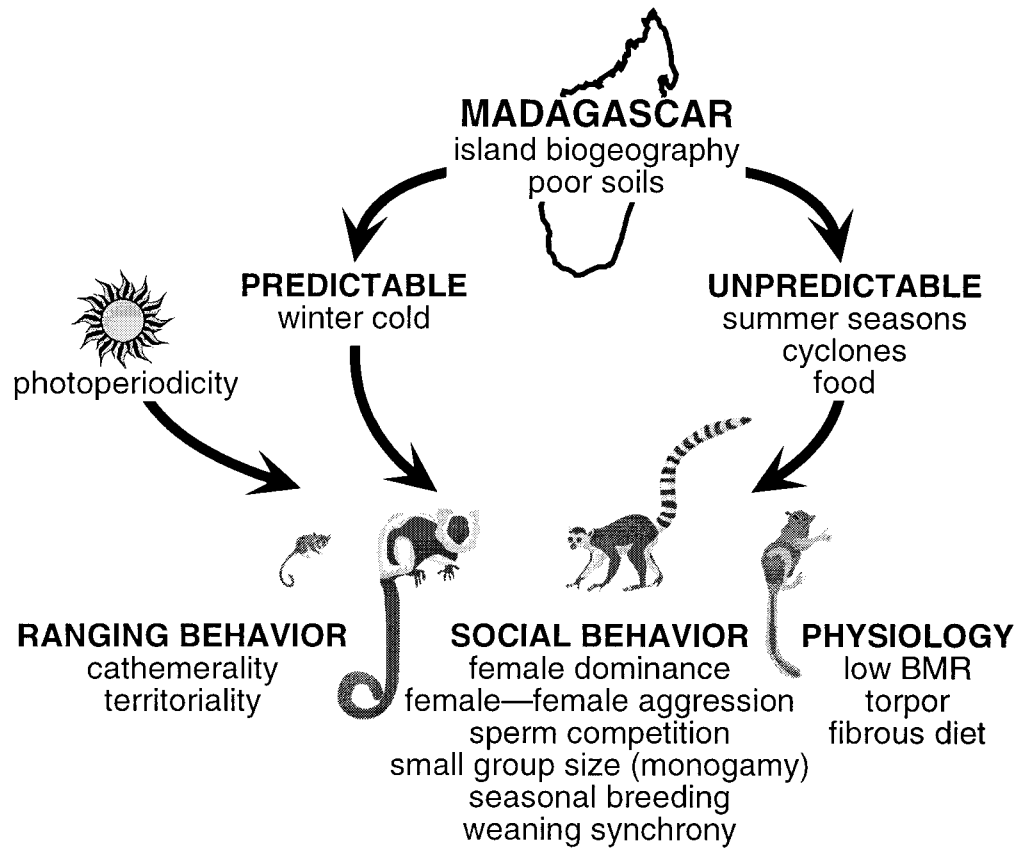


Fig. 5. Lemur strategies to maximize fitness in the energy constrained environment of Madagascar. The combined effect of poor soils and island climate have generated scarce and unpredictable resources. According to this "energy frugality" hypothesis, the majority of lemur traits are adaptations to conserve energy (e.g.,

low BMR, torpor, sperm competition, small group size, seasonal breeding) and to maximize use of scarce resources (e.g., catheimerality, territoriality, female dominance, fibrous diet, weaning synchrony). Only photoperiodicity and winter season are predictable due to the southern latitude of Madagascar.

horn et al., 1999a). While small group size may make the available resources last longer, the targeted female-female aggression may be attributed to contest competition for scarce resources (Wright, 1995; Pereira and Kappeler, 1997).

Hypometabolism, including hibernation and torpor in small lemurs, may be an adaptation to the scarce resources of winter (Petter-Rousseaux, 1980; Schmid, 1998; Schmid and Ganzhorn, 1996; Schmid and Kappeler, 1998). Another very seasonal behavior in lemurs, breeding, will in itself conserve energy dedicated to reproduction. But the breeding synchrony within a species may be geared also to maximize food quality

and availability during weaning (Sauther, 1991; 1998; Meyers and Wright, 1993; Pereira, 1993a,b). The example from the eastern rain forest site, Ranomafana National Park is indicative. Although each species gives birth synchronously, different primate species do not give birth in the "spring," but rather give birth in different months over a 6-month span from June to December (Fig. 3). One reason behind this interspecies birth asynchrony could be a preference for weaning that happens in all of the species when fruits, new leaves, and insects are likely to be abundant. Crafting life history calendars of different sized lemurs to target weaning in the time of abun-

dance is a fine-tuning between primate and environment that has not been observed to such a narrow degree in other primate communities. This suggests that the environment in Madagascar has more well-defined constraints than other continental areas where primates have evolved (Fig. 5). Although it has been suggested that weaning is a "key life history trait" (Lee et al., 1991; Meyers and Wright, 1993; Lee, 1997), the life history calendar of the sympatric lemurs from the rain forest of Madagascar, presented here, is a strong example of how crucial this weaning is to survival.

This maximization of scarce resources extends to the evolution of special physiological and morphological adaptations that assist in avoidance of interspecific competition for food, such as ever-growing incisors with long extractive fingers in aye-ayes (Erickson et al., 1998), cyanide tolerance in golden bamboo lemurs (Glander et al., 1989; Tan, 1999), and digestion of low quality browse in sportive lemurs (Ganzhorn, 1993).

The alternative hypothesis to scarce resources influencing behavioral adaptations (ECH and EFH), is the evolutionary disequilibrium hypothesis (EVDH), which suggests that changes in behavior, such as diurnality and group size, have been caused by the extinction of the giant raptor predators within the last 500–1,500 years (van Schaik and Kappeler, 1996). The hypothesis suggests that diurnality of lemurs is recent, and that the cathemerality (both day and night activity) of some lemur genera is a transition phase between nocturnality and diurnality (van Schaik and Kappeler, 1993). The EVDH suggests that smaller group size, abundance of monogamous social structures, lack of sexual dimorphism, and lower metabolic rate are all a result of the recent nocturnality of the diurnal lemurs, not a result of scarce food resources or other ecological constraints (van Schaik and Kappeler, 1996).

The limitations of the proposed model have been pointed out by field studies of cathemerality (Overdorff and Rasmussen, 1995; Overdorff, 1998; Colquhoun, 1998; Rasmussen, 1999), group composition of diurnal species (Sussman, 1992; Richard et al., 1992;

Wright, 1995; Vasey, 1998; Balko, 1998), and studies of predation (Sauther, 1993b; Goodman et al., 1993; Wright, 1998; Karpanty and Goodman, in press). Further evidence that does not support the EVDH is that nocturnal species outside of Madagascar do not show female dominance, and therefore female dominance is neither the ancestral condition, nor necessarily related to a transition phase into diurnality. Obviously, it is difficult to estimate how long it takes for new behaviors to evolve, but in the case of lemurs and EVDH, a broad range of traits, all seen in both nocturnal and diurnal large- and small-bodied lemurs, would have evolved quickly (within 500–1000 years). More comparative field data is needed to evaluate how much of lemur behavior is likely to be ancient or recent, hence EFH or EVDH. It is quite likely that lemur societies have changed substantially during the last 500–1,500 years with the extinction of community members, but how much of the change has to do with the basic lemur traits remains in question.

#### Future directions

Although we have learned much about primate evolution from comparing these new field and captivity data on lemurs with the anthropoid primates, many questions remain. Further research comparing aggression, predation, and dominance in wild population under different ecological conditions may further elucidate the effect of environment on behavior. With new field techniques using fecal analysis, it is now possible to accurately document reproductive patterns of both male and female lemurs (Schideler et al., 1993; Brockman and Whitten, 1996; Wasser, 1996; Brockman et al., 1998; Whitten et al., 1998), and these new studies, coupled with paternity analysis, could focus our studies of behavior and clarify behavioral explanations more fully than possible in the past. Many lemurs have specialized physiological adaptations, such as being able to daily consume large amounts of cyanide-filled bamboo or being able to store fat for hibernation (Glander et al., 1989; Tan, 1999; Muller, 1999b), which if studied under controlled conditions, may give us insights into their mechanisms and evolution. Research

on vocal and chemical communication among lemurs might focus on interspecific competition and common responses to interspecific predator alarm calls (Macedonia, 1990; Macedonia and Stanger, 1994; Zimmerman, 1995; Buesching et al., 1998; Hafen et al., 1998).

Single or double species studies of behavior and ecology over annual cycles have elucidated seasonal patterns in lemurs, but future research might concentrate on a more community approach to lemur behavioral ecology (Fleagle and Reed, 1996; Stevenson et al., 1998; Chapman et al., 1999; Ganzhorn et al., 1999a; Wright and Jernvall, 1999). Examining the effects of multiple predators and interference competition on the behavior and demography of intact lemur communities may give us insights into lemur evolution. Understanding the changes in behavior and ecology of lemur communities in fragmented and disturbed forests may give us insights into the behavior, ecology and needs of diminishing populations. Comparing the long-term demography and population genetics of intact lemur populations with populations in disturbed habitats, will give us data to influence effective conservation planning. The effect of parasites and disease on wild populations will give us information needed to manage disturbed populations. Patterns of modern biogeography should be better known, including census of lemur population densities in widespread areas, coordinated with plant distribution data using GIS and satellite photographs. Conservation management would benefit from studies of lemurs ecological roles in the forest (Jernvall and Wright, 1998), including pollination; predation on leaves, seeds, and insects; and seed dispersal to better understand the value of lemurs to forest composition and regeneration (Kress et al., 1994; Ralisoamalala, 1996; Scharfe and Schlunde, 1996; Hemingway, 1996; Overdorff and Strait, 1998; Dew and Wright, 1998; Ganzhorn et al., 1999b).

In the future, we need a more integrated approach to research, combining data from both laboratory and field, disturbed and undisturbed habitats, using and developing new technologies. Perhaps with the combined cooperation of physical anthropolo-

gists, tropical ecologists, botanists, physiologists, nutritionists, parasitologists, chemists, reproductive biologists, behavioral ecologists, and conservation biologists working together to concentrate on understanding lemurs in the context of the Malagasy environment, we can both learn about this specialized group of primates, and how to best save them for future generations.

### Implications for lemur conservation

The intricacy of the lemur adaptations that have evolved to cope with the environment of Madagascar may have left lemurs vulnerable to large environmental changes, such as the arrival of humans. The paleontological history has showed tremendous losses of both forests and lemurs since the arrival of humans to Madagascar (Godfrey et al., 1997a; Lowry et al., 1997). One-third of lemur species has already suffered extinction. Still remaining lemurs are vulnerable to human disturbance, such as selective logging, in addition to the continuing threat of deforestation of Madagascar (Mittermeier, 1988; Mittermeier et al., 1994; Sussman et al., 1994; Wright, 1992, 1997a; Ganzhorn, 1995; White et al., 1995; Ganzhorn et al., 1996; Richard and O'Conner, 1997). Lemur populations in heavily fragmented or logged habitats are more at risk from devastation by climate factors such as drought or cyclones because they lack the "insurance" of being able to retreat into larger forested areas and may also suffer from reduced genetic variability (Arnaud et al., 1992; Merenlender, 1993; Pope, 1992, 1996, 1998; Rabarivola et al., 1998; Scheffrahn et al., 1998). The balance between a specialist predator and prey could also be tipped by human impact, causing an abundance of either predator or prey, a problem for the population of lemurs or the forest (Wright et al., 1997). Because of the seasonal breeding patterns of lemurs, populations may be unable to recover from either increased mortality or decreased food availability.

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